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# PLANT LIFE

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# PREFACE

I HAVE not attempted in this little book to cover the whole ground indicated by its title. My object has rather been to try to place before the reader a few of the salient features of plant form from the point of view of function. In this way, as I think, it is less difficult to keep in mind the general nature of the causes which have been operative in bringing about the marvellous beauty and adaptedness of form which is so apparent in every branch of the vegetable kingdom.

The task of selection has not proved an easy one, and nobody can be more fully alive to the imperfections of treatment, and other sins of commission and omission, than I am myself. Some, at any rate, of the last-named defects are attributable to the limitations of space.

I have deliberately touched, though with enforced brevity, on certain of the more difficult problems which are even now confronting us, and I have endeavoured to present them with as little technicality as possible, but whether I have been successful in this I must leave to the judgment of others.

It is not impossible that some readers will expect to find much that is absent from this little book—but it seemed better to utilise the space at my disposal by devoting it to matter not so generally discussed in a volume of this size, than to attempt to say again what has already been well done in other works of this scope.

In conclusion I wish to express my thanks to Mr. Tabor and to Mr. Trowbridge for the assistance they have kindly given me in the preparation of nearly half the illustrations.

J. B. F.

*Gerrard's Cross,*
*Feb.* 20, 1913.

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# PLANT LIFE

## CHAPTER I

### INTRODUCTION

A general survey of the Animal and Plant kingdoms emphasises in the clearest manner the cardinal importance of the great functions of nutrition and reproduction. It also enables us to perceive the intimate relation which exists between the full discharge of these functions and the evolution of the higher from the lower forms of life. We are further led to conclude that there is no great gulf separating the animal from the plant, but that the similarities which exist between the two great classes of living things are even more striking than are the obvious differences, at any rate in so far as essentials are concerned. Indeed, the differences consist in features which are, after all, mainly of secondary importance, and they are largely determined by the divergent methods of obtaining food which characterise the animal and the plant respectively.

Casting our glance still further afield, the boundary line between the organic and the inorganic worlds now appears less sharply defined than formerly, and many reactions which used to be regarded as immediately and essentially associated with life and active vitality are now recognised as being susceptible of a less mystical interpretation. Thus it has become more and more clearly apparent during the last few years how great a share the various ferments may take in promoting those reactions which formerly were regarded as inseparable from the living organism.

Now although these ferments, in the narrower sense, are doubtless the products of protoplasmic activity, they can initiate and carry out their specific reactions in a test-tube under conditions which are incompatible with the concurrence of life in the ordinary, or indeed in any real, sense of the word. Evidence is accumulating to show that the ferments owe their specific activities to their physical structure, and that they approximate to the singular class of " catalytic " inorganic bodies, which, like them, are able to promote and accelerate certain chemical changes without themselves undergoing destruction.

Indeed, as time goes on, exact investigation is continually lifting corners of the curtain which conceals the mysteries of life, and the glimpses we have caught tend to suggest that although the reactions which are going on in the living laboratory are (at present) incalculably more obscure than those with which we have, in a measure, become familiar in ordinary chemical and physical researches, nevertheless they are similarly influenced by physical conditions, and they obey the same chemical laws. The chief differences between the reactions in the living body and those which occur outside it seem to lie mainly in the greater complexity of the substances concerned, as well as in the necessity for accurate adjustment of the reacting substances towards each other in ways which we can at present but feebly imitate. An important feature in this matter of adjustment consists in that state of aggregation which we call *colloidal*, which is so characteristic of the framework of living things, and by virtue of which the physical conditions for many chemical reactions are provided.

A simple example perhaps may serve to make the point clearer. A piece of platinum *wire* will not bring about the ignition of a mixture of coal gas and air, but if the platinum be *finely divided*, e. g. in the form known as " platinum black " or spongy platinum, it will do so. If the platinum be still further divided, it assumes the condition known as " colloidal platinum," and it is then capable of promoting many other chemical changes in a manner closely resembling, and perhaps essentially similar to, that characteristic of many organic ferments.

Of course it is not meant to suggest that the complex phenomena of life are at once reducible to terms as simple as those which regulate the reactions just indicated, and it is beyond all doubt that much more refined investigation than our present knowledge renders possible will be needed ere we shall solve the ultimate secrets of life, if indeed we ever are able to do so. But we shall go far by employing the methods which have already taught us so much, methods which consist in exact experiment and accurate analysis.

The principal reason why our knowledge of the *modus operandi* of the living organism is so largely lacking in precision lies just in the vast range of the materials with which we are there dealing, and in the consequent difficulty of analysing the results of our experiments sufficiently to be able to refer them to their real causes.

But although it may not be possible as yet to explain the great majority of the life processes, either of animals or of plants, it will soon be apparent that relatively simple chemical and physical processes have profoundly modified the course of evolution of structure and form. This is more obvious, perhaps, in plants than in animals, because the retention of relatively simple mechanisms in connection with the absorption of food materials has kept the plant free from the complications introduced by the development of specialised locomotory activity, and the concomitant elaboration of a nervous system.

# CHAPTER II

## THE PLANT AND ITS FOOD

One of the most striking points of difference between the animals and the plants consists in the evident and purposive motility of the former, and the apparent (but only apparent) immobility of the latter. Nearly all animals more or less actively seek their food, and ingest it in a solid form; and even those species which, like the adult oyster, are tolerably stationary, nevertheless exhibit some sort of motion by which currents of water, bearing particles of food are drawn into their bodies.

The general tendency in the plant kingdom, on the other hand, has been to produce relatively stationary forms which do not actively pursue their food, but passively absorb it from their surroundings. Many of the most primitive plants, however, share with the animals a faculty of vigorous locomotory movement, swimming through the water in which they live by means of vibratile filaments or *cilia*. What is it, then, which has caused the higher members of the one kingdom to abandon this locomotory activity while those of the other have not only preserved it, but have acquired all the accessory complications of structure that purposive motion necessarily entails ?

The answer is to be sought in the results of an apparently trivial difference in structure between the animals and plants which made its appearance at an early period in evolutionary history. It is a difference which from the start was fraught with consequences of the greatest importance, and has profoundly affected the entire course of development in the two kingdoms respectively. Stated simply, it consists essentially in this, namely, that the living substance of the plant secretes over its surface a skin of cellulose, or some analogous substance, whilst that of the animal does not.[1]

If we examine any one of the simplest microscopic individuals of whose vegetable nature there can be no dispute, we shall find that the protoplasm, or living substance, is enclosed in a not-living skin or bag of cellulose. This skin is not an indispensable structure, for the living substance may, for a time at least, exist without it. Even in the highest plants this commonly occurs during the first stages of embryonic existence, but as soon as development begins the membrane is

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[1] This statement is broadly true, for although cellulose is not unknown in the animal kingdom it has never been so arranged in the body as to affect the whole relations of the animal to its physical environment as it does in plants.

secreted over the surface of the living substance, which is henceforth shut off from the outer world throughout the vegetative life of the individual. It is usually in connection with certain reproductive processes only, as, for example, when a new generation is about to arise, that the plant-protoplasm is more or less freed from the cellulose skin with which it is almost invariably clothed at other periods of its existence.

The simplest method of realising what all this means to a plant is to study some definite example, when other salient features of plant life will also come directly under notice. For this purpose one of the common lowly plants belonging to the *algæ* may be chosen, and we will select as an example a microscopic organism belonging to the genus *Chlamydomonas*.

This plant is of fairly common occurrence in ditches and pools, especially in late spring and in the autumn. Its body consists of a single cell, that is to say its somewhat oval-shaped protoplasm is contained within a single membranous cavity. At one end two vibratile hair-like filaments of protoplasm, called cilia, project through the membrane, and it is by means of these that the little plant is able to swim actively through the water in which it lives. Within the protoplasm of the body, and just beneath the spot where the cilia sprout from it, are two contractile vacuoles—hollow spaces filled with

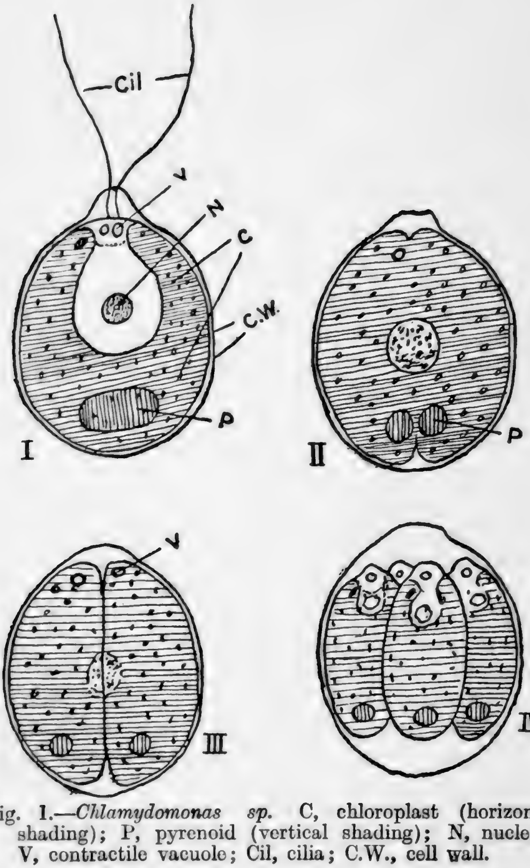

Fig. 1.—*Chlamydomonas sp.* C, chloroplast (horizontal shading); P, pyrenoid (vertical shading); N, nucleus; V, contractile vacuole; Cil, cilia; C.W., cell wall.

liquid which are continually contracting and expanding. This kind of vacuole is also characteristic of many of the primitive animals, whilst it is only met with in comparatively few of the more primitive and still motile plants. A small, somewhat refractive, spot in the protoplasm marks the position of the nucleus, an important structure which is found in the protoplasm of animals and plants alike. Another part of the protoplasm is coloured green, and is clearly defined from the rest of the living substance not only by its colour, but by its denser consistency. It is termed the *chloroplast*, and it often contains a clear spot in its interior, termed the pyrenoid. Finally, close to the point of insertion of the two cilia, there is a small brown or yellow "eye-spot." The little plant swims about through the water, and though the movements appear at first sight to be aimless, they are not altogether so, for if a large number of individuals are present, so as to give the water a green tinge, it is seen that they congregate on the illuminated side of the vessel. That is to say, they are affected by the *stimulus of light*, and the members of the colony spread themselves out towards the source of illumination. In other words, they are *irritable*, which is the technical way of expressing the fact that they are capable of responding by a movement to a stimulus—in this instance, to the stimulus of light.

Under suitable conditions of temperature and nutriment the Chlamydomonas plant rapidly multiplies in a vegetative or non-sexual manner. This is brought about by the division of the protoplasmic contents, within the membrane, into a number of smaller lumps, each of which becomes a small image of the original parent. They are commonly two, four, or eight in number, and finally escape from the ruptured membrane of the "mother cell" into the surrounding water where they grow, and may give rise in their turn to new individuals.

Now such a plant as Chlamydomonas is relatively very simple, and yet it already exhibits the most striking characters that distinguish the majority of plants.

In the first place its living substance is enclosed in a membrane, and in the second its protoplasm contains a green chloroplast. In order to grow it must clearly obtain food, but the presence of a membrane precludes it from acquiring any except such as is already dissolved in the water. No solid particles can pass the membrane and so reach the protoplasm, but water and substances dissolved in it will readily do so. The whole of the mineral food substances, and such gases as oxygen and carbon dioxide, reach the protoplasm in this, and only in this way.

But this external membrane not only limits the nature of the food-supply, but as the size and complexity of the body increase, it continues more and more to restrict the kind of movements which make for locomotion. Such movements indeed soon come to lose their value, even in water plants, when the capacity for ingesting solid food has been lost, whilst they would tend to render the existence of a land flora practically impossible.

We may consider Chlamydomonas, then, as a plant belonging to a class the members of which have not as yet diverged far enough along the plant line of evolution to have lost the power of movement. But even amongst the near relatives of the species under consideration there are forms which pass at least a part of their vegetative lives in the passive and non-motile condition characteristic of more advanced members of the vegetable kingdom. A familiar example is afforded by the green incrustation everywhere to be seen on old damp palings. This incrustation consists of countless numbers of minute green cells known as *Pleurococcus*, which grow and multiply by division. The separate individuals are habitually destitute of all locomotory mechanism, and each grows and multiplies in the spot where it happens to have become fixed.

The Pleurococcus plant thrives in damp air, and it depends on the chance supplies of moisture for the water it requires. The gases of the atmosphere, passing by diffusion through the membrane or *cell wall*, are dissolved in the watery sap which bathes its living protoplasmic substance. Thus supplied with food materials, it multiplies rapidly. When an individual has reached a certain size it divides into two, and this process being repeated in the various individuals of a colony the Pleurococcus spreads rapidly over the surface of the damp wood. Furthermore, the individual plants withstand desiccation without dying, and in this condition they are carried by currents of air to fresh spots where new colonies can be started.

But to return to Chlamydomonas. Its second feature of importance, from our present point of view, consists in its greenness.

As we have seen, the green colouring matter, or *chlorophyll*, is not diffused through the whole protoplasm, but is restricted to one or more (in this plant, one) definite and specialised masses or corpuscles, each of which constitutes a *chloroplast*. The part which the chloroplast plays in the cell [1] is that of utilising the energy

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[1] CELL.—This is the term commonly used to denote the unit of a living organism, though, unfortunately, it is not always used in the same sense by different writers. In this book it will be taken to denote a *mass of protoplasm* (whether enclosed in a cellulose membrane or not) *which is dominated by a single nucleus.* This protoplasmic mass is commonly, but not necessarily, separated by a cell membrane from other similar ones in the cell-aggregates which together constitute the bodies of larger plants. A plant may thus consist of (1) a single cell; (2) a number of coherent cells, each more or less delimited from the rest by a membranous envelope or partition wall; (3) a number of coalescent cells, consisting of protoplasmic units, each containing one nucleus, but the units *not* separated from each other by cell walls. Such a cell colony

of sunlight, which enables it to construct complex carbon compounds when supplied with the raw materials, carbon dioxide and water. In other words, the chloroplast is a mechanism which is able to build up carbon compounds which are poorer in oxygen than are the raw materials upon which it works, and thus the kinetic energy supplied by the sunlight becomes converted into the potential energy represented by the chemical products which are formed as the result of chloroplastid activity. This energy (which was derived from the sun), can again be released by oxidation, that is by more or less rapidly *burning* those products. It may then be utilised to heat a furnace, to drive a steam engine, or to maintain the bodily processes of a man.

This property of the chloroplast is of fundamental importance, not only for the plant, but for animals as well, for every animal is directly or indirectly nourished by vegetable products, which form the starting-point of the food-supply of the world. In the absence of chlorophyll there would be none of the higher plants as we know them, nor would there, in all probability, be any of the higher animals at all. In this sense we are indeed all children

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may be termed a *syncytium*. It must be borne in mind that the membrane is not an *essential* feature of cells, although in plants, as stated in the text, it is of very general occurrence. The cell contains other bodies, *e. g.* chloroplasts, starch, oils, etc., but these are non-essential, and are often absent.

of the sun, for its energy, reaching us through the mediation of the plant, is the *fons et origo* of our existence. How, then, does the Chlamydomonas proceed by means of its chlorophyll to make these more complex food substances ?

Although we are not as yet fully acquainted with all the steps of the process, we already know enough to enable us to sketch in outline the main sequence of events. Putting the story in its simplest form, we may say that the carbonic acid, which is formed when carbon dioxide dissolves in water, is continuously broken up as the result of the action of sunlight of a suitable intensity upon the chlorophyll of the living plant. Oxygen is liberated, and organic compounds, usually sugars, are produced inside the cell. When the reaction is sufficiently rapid, so that the concentration of sugar reaches a certain strength, starch often makes its appearance, but it is merely a secondary product, depending on the prior formation and accumulation within the cell of sugar in sufficient quantity. The earlier stages of sugar formation are still obscure, but there is little doubt that formaldehyde (the formalin of commerce) is produced during the process. This substance has been used as the starting-point for the synthesis of sugars in the laboratory, and although it is difficult to detect it with certainty in the plant there are strong reasons for considering that it really is formed as an intermediate product, but it is so rapidly changed to a more complex molecule that only very minute quantities of it are present at any given instant. Such a rapid change would indeed be anticipated, as formaldehyde, even in small quantities, is a violent poison, that is, it speedily reacts with ordinary protoplasm in such a way as to destroy the intimate chemical architecture of the living substances. The mere fact of its poisonous character constitutes no objection to its occurring as an intermediate substance in the synthetic process; we know of many other compounds which, though deadly poisons under certain circumstances, are still normally present in various phases of the transmutation of substances going on within the plant or animal body.

Inasmuch as this synthesis of sugar, by means of the chloroplast, is normally dependent on suitable illumination, the process is commonly called *Photosynthesis*,[1] a much better term than the older expression, *Carbon assimilation*, by which it was formerly known.

Since Chlamydomonas is a motile organism, it can and does move through the water in which it lives in such a way as to become exposed to the best conditions of illumination. This faculty of taking up a suitable position

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[1] Even Photosynthesis is not an altogether satisfactory term, for there are strong reasons for believing that although light *starts* the process, it is not concerned in the further synthetic processes that result in the formation of sugars.

as regards the direction of the light is, however, a very widespread one, and we shall meet with it again, although in a modified form, in studying the behaviour of the highest plants; for the property of irritability which in Chlamydomonas finds expression in the independent movement of the organism as a whole, is a necessary condition of existence for every plant to a greater or less extent. Only in this way is it possible for it to place itself *en rapport* with a variable and changing environment, and hence with the physical conditions under which it lives.

A brief survey of the more salient physical characters of chlorophyll will not be out of place here, inasmuch as they stand in suggestive relation to the properties of this remarkable substance.

It is easy to extract the green colour of plants by soaking a quantity of grass in strong alcohol. A dark green liquid will thus be obtained which if examined by *reflected* light will appear to be not green, but blood-red in colour. This property of "fluorescence" is not confined to chlorophyll, but is shared by many other organic and some inorganic substances, and it affords useful hints as to their more intimate chemical architecture. A solution, prepared by the rough-and-ready method indicated above, is of course not pure chlorophyll, but it contains several other colouring matters which can be separated from it by appropriate means.

A solution of chlorophyll examined by means of a spectroscope exhibits a number of very definite *absorption bands*, due to the absorption of certain of the coloured rays of the spectrum (= the dark bands) while the rest of the light filters through and is unaffected. There are two very dark bands in the red region of the spectrum, and others, mostly fainter and more diffuse, in the yellow, green and blue-violet regions. Furthermore the extreme red and the violet end of the spectrum are also obliterated.

It is found, as might perhaps be anticipated, that the rays of light which correspond to the dark absorption bands in the *red* region of the spectrum are those principally concerned in promoting photosynthesis. The other rays which are absorbed are not indeed without influence, but they are of comparatively little consequence from the point of view with which we are just now concerned. We see from the foregoing why it is so essential that the chlorophyll in the living plant should be directly exposed to the light from the sky, inasmuch as any light which has already traversed a layer of chlorophyll will have been deprived of those rays that are essential for photosynthesis. Such "filtered" light will of course be unable to develop photosynthetic activity in a chlorophyll-containing organ or organism that may be exposed to it. The apparent exceptions afforded by plants which flourish in deep shade are due to the circumstance that they are able to utilise light of low intensity which pases through the *interspaces* of the leaves of the trees above.

It turns out also that the chlorophyll green is destroyed by the same rays that are photosynthetically active, and this destruction is without doubt intimately connected with its function in relation to such rays. It does not, however, follow, nor indeed is it probable, that the rôle of chlorophyll is a very direct one in influencing all the stages of photosynthesis. It is more likely that its primary function is concerned with the earliest stages, utilising the energy of the absorbed light, and thus providing the conditions for starting those processes of chemical change which, under the influence of protoplasm, culminate in the formation of the higher carbon compounds. For, so far as is certainly known, it is only when chlorophyll is united with the living substance that these higher compounds are able to make their appearance.

When the green chlorophyll matter is decomposed in a living plant cell, other colours, commonly red or a rusty orange, make their appearance. A striking example of this is furnished by the red snow plant, *Hæmatococcus nivalis.* This unicellular alga is closely related to species of Chlamydomonas, and indeed by some writers is included in that genus. It exists in a green and a red form, and is either motile, like Chlamydomonas, or it may pass into a non-motile resting stage, when it will withstand complete desiccation. When it is grown in water containing traces of available nitrogenous food it is green, thrives, and multiplies rapidly, but if the supply of nitrogenous food is used up, the rate of increase drops, and the plants change colour, owing to the degradation of the chlorophyll and the corresponding development of a reddish pigment. When it has reached this condition the addition to the water of a small supply of nitrogenous food, such as a crushed fly, rapidly brings about the restoration of the green colour in the cells. When found growing on snow-slopes, the red tint is obviously due to the absence of available nitrogenous food, possibly coupled with the conditions of intense illumination and low temperature prevailing in such situations, for when the plant is once more suitably nourished the green colour soon re-appears.

To sum up, then, what we have learned of the significance of chlorophyll, both to the plant and to the world at large, we may say that its primary function is to enable its possessor to synthesise important complex foodstuffs from very simple raw materials; in other words, that a part of the energy contained in the sunlight is rendered available for the use of the plant. Furthermore, that the sugars or their representatives thus formed, provide the starting-point for still other reactions which go on within the body. They more directly supply the energy which renders possible the production of those almost infinitely complex substances which form the very substratum of life itself.

## CHAPTER III

### EVOLUTION OF CELLULAR STRUCTURE IN SIMPLE PLANTS

Emphasis has already been laid on the circumstance that the plant cell, owing to the presence of its investing skin of cellulose, is only able to absorb and use substances capable of diffusing through the membrane. Consequently food from without can only reach the protoplasm in solution. Salts and other solid food materials are invariably absorbed in a state of solution, and the same is true of gases, such as oxygen and carbon dioxide, as well.

But water has other functions to discharge within the plant, besides that of serving as a vehicle for the intake of nutritive materials. It serves to maintain the protoplasm itself in that characteristic semi-fluid condition which is essential to the exercise of its vital functions. In the absence of sufficient water-content the protoplasm may actually die. Even if it is able to tolerate comparative desiccation, it passes into a state in which all vital reactions are slowed down until they are practically brought to a standstill.

We see clearly, therefore, that an adequate water supply must be regarded as a primary condition of all active life—prior in importance even to the provision for photosynthesis in the green plant. For when water is cut off, the building up of complex carbon compounds is *ipso facto* arrested, however completely all other conditions of photosynthesis may be satisfied.

It is clear that plants which pass the whole of their lives in a watery medium are not confronted with the risk of water starvation, but this danger may, and often does, become acute as soon as they exchange a purely aquatic for a terrestrial habitat. It is no exaggeration to assert that the most salient features in the structure, and the behaviour of green vegetation in general, is mainly connected with a solution of the problems presented by water requirements on the one hand, and by those of photosynthesis on the other. It is in relation to these two overwhelmingly important functions that vegetation has assumed much of its present form, for any plant failing to achieve success in these two directions must either suffer extinction, or must obviate the inevitable difficulties of existence in another way altogether. Some, like fungi and many parasites, have adopted the latter alternative; but as regards the vast majority of the green plants, we shall find that a recognition of these two dominating factors, water and light, will serve us in good stead, as furnishing an important clue to much of the complexity of *structure* to be observed in so many of the more advanced types of plants. Such complexity is intimately related with a corresponding differentiation and specialisation of *function*, and indeed it is largely to this circumstance that many of the more striking examples of " adaptation to the environment " are to be attributed.

The best way of arriving at a clear conception as to how the higher plants, with their complicated structure and high degree of differentiation, have come into existence in past times, is to study the more primitive types which illustrate various degrees of advance on the simple unicellular stage. The class of Algæ, which includes the simpler water and land plants, will furnish us with excellent material wherewith to reconstruct, in outline at least, the course of vegetative evolution. This must not, however, be taken to imply that the simple types in question are to be regarded as new forms which are *now* on an upward grade of evolutionary development. They are to be understood, rather, as permanent representations of some of the phases through which the ancestors of the higher plants have almost certainly passed. They may be regarded as morphological survivals that have slipped out from the main stream of evolution into the quiet backwaters of life, preserving in themselves the types and forms of a vegetation that otherwise might well have passed into oblivion. Furthermore, whilst they may be, and often are, admirably fitted by their very simplicity and variety to certain kinds of surroundings, they are not suited for a life under other conditions which demand a more highly specialised body.

As a matter of fact it is far from easy to define very exactly what is meant by "higher" and "lower" types respectively. We commonly associate the ideas of specialisation and differentiation with the higher types. An obvious adaptation to a particular environment is often taken as a sign of high organisation, but in reality very many of the extremely simple plants are admirably adapted to their particular surroundings. Moreover, we are acquainted with numerous species which at the present time are simple because they have lost the complexity of structure formerly possessed by their ancestors. We often speak of these as degraded forms; but parasites, which illustrate this point very well, are frequently admirably adapted by their very simplicity of structure to their particular modes of life. In practice, however, we can generally distinguish between what is primitively and what is secondarily simple, and all that need be said here about the matter is that in any classification of this sort most people more or less unconsciously adopt an anthropomorphic standpoint and standard. Provided we recognise this for ourselves, we shall avoid confusion of thought, and our mental picture will be the clearer.

Within the genus Chlamydomonas, which we selected as an example of a primitive plant, we find that some, at any rate, of the species are able to manifest a change of form and character according to the circumstances under which they are growing. This fact will serve as a starting-point from which to trace the development of complication of form and structure in the plant kingdom.

Individuals belonging to certain species, e. g. *Chlamydomonas Braunii*, when cultivated on appropriate nutritive media, such as a relatively concentrated solution of mineral salts, or on a damp substratum, cease to multiply in the ordinary way. Instead of the cells which have been formed by the division of a parent-cell becoming separated and swimming away, they remain cohering together. Their cellulose walls swell up and form a gelatinous mass in which, as in a matrix, the cells (*i. e.* the nucleated protoplasmic units) which have arisen by the repeated fission of parent cells remain embedded. Even the cilia may become enveloped by the swelling jelly, and they may even entirely disappear. The cell colonies thus consist of motionless masses of green jelly. But there is as yet very little *organisation* in such colonies. The form of the mass is not constant, and a return to what may be termed normal conditions of life may readily lead to a complete disruption of the colony, the individual cells escaping from the jelly and returning to the unicellular motile condition which is in the main characteristic of this group of algæ.

This tendency to form agglomerations of individual cells is carried to a far greater degree of perfection in some other groups of the lower algæ. Thus *Apiocystis Brauniana* (Fig. 2), an alga fairly often to be met with in ponds, attached to larger algæ and other objects, consists of a pear-shaped mass of jelly in which are scattered masses of chlorophyll-containing protoplasm. The little protoplasmic spheres, which represent the living part of the individual cells composing the Apiocystis plant, are grouped in the more peripheral parts of the gelatinous matrix formed by the swelling of the common cell walls. Each cell (see footnote on p. 20) is furnished, like Chlamydomonas, with a pair of cilia, but these have ceased to be functional, for they are enclosed in a thin projection of the gelatinous wall. When examined attentively, it can be observed that the individual cells, or *protoplasts*, are multiplying by fission. This is betrayed by their aggregation in pairs and groups of cells which have obviously sprung from a single parent. But an interesting and important feature of their development consists in the fact that, after

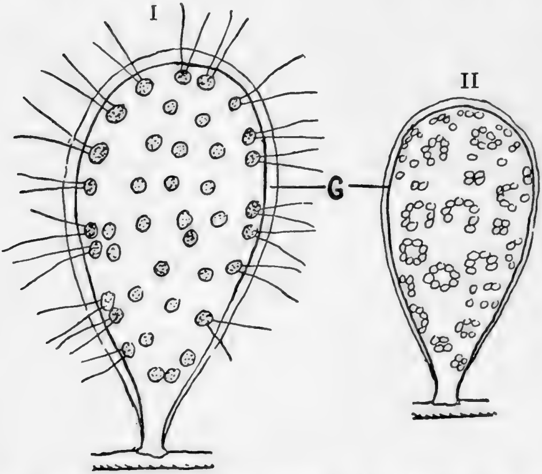

Fig. 2. — *Apiocystis Brauniana.* I. — Mature Plant. II.—Younger Plant. G, The gelatinous outer layer of the membrane.

they have been formed, they can modify their positions. Thus all of them come to lie just beneath the periphery of the jelly, and are not uniformly distributed through it as might have been expected. This arrangement is one which secures evident advantages from the point of view of suitable illumination.

We see here a simple example of *co-ordination* between the cells of an organism. It is true that it is of a very rudimentary kind, but the fact that an organism, originating in this manner, possesses a definite form at all, is a clear proof of its existence.

The form of Apiocystis seems to be fairly constant, but when conditions are suitable, some or all of the protoplasts may escape from the gelatinous sheath and swim away as biciliate Chlamydomonas-like organisms, though they are destitute, for a time at least, of even a cell membrane. In this condition they are known as *Zoospores;* when one of them settles down it becomes invested in a cell wall secreted by the protoplasm, and by repeated fission builds up another Apiocystis plant. This mode of reproduction by means of zoospores is very common in the algæ, and it serves to recall the early stages in the history of the race which is thus repeated during the beginning of the life of a new individual.

Now a pear-shaped organism is, by its very form, rendered incapable of reaching a large size, at any rate without such accessory complications as are not to be thought of in connection with primitive plants. There are other lines of development which have proved more fruitful from an evolutionary point of view, and of these the flattened expansion and the filamentous types represent the most successful. Indeed, it is on these lines, or rather on a combination of both of them,

Fig. 3.—*Ulva lactuca*, the Sea-Lettuce.

that the development of the higher forms of vegetation has mainly advanced.

The group of algæ to which belongs the green sea-lettuce, so common on some of our coasts, especially where the sea-water is contaminated by sewage effluents, furnishes beautiful examples of the simpler stages in the evolution of a flattened leaf-like type of thallus. Ulva, the sea-lettuce in question (Fig. 3), is somewhat advanced, for it consists of cells which are arranged in two layers, but otherwise division occurs in the cells of each layer in such a way as to increase the area of the surface. The multiplication of cells is not very uniform over the whole surface, those nearer the margins dividing and growing faster than those nearer the middle line of the leaf-like plant. Thus the surface of the frond is thrown into folds and wrinkles as the necessary consequence of this unequal growth. But that there is some co-ordinating influence at work amongst the cells is shown by the fact that this wrinkling does not become excessive, and the plants assume a fairly definite *form* which makes any given individual easy to recognise as belonging to this and no other species. The Ulva plants are securely anchored to stones and other supports by a special development of the cells near the base of the plant. These grow out into long filamentous strands, and adhere very closely to the surface of the rock. The specimens one often sees washed up after a storm are usually the upper parts of the plants, which have become torn off by the waves.

So far we have only considered aquatic forms of algæ, but there are certain kinds which grow in damp situations on land. Amongst these is Prasiola, which is not unfrequent in certain localities (Fig. 4). Its body is composed of a leaf-like expansion of cells which lower down form a contracted stalk-like body attached to the soil by means of special filamentously elongated cells called rhizoids. The cells which compose the substance of the thin leaf-like body are all alike, but the common walls, as befits a terrestrial organism, are more cartilaginous and tough than those of the more aquatic types. Even reproduction is correlated with the change of habitat from water to the land. The cells which become detached from the frond are

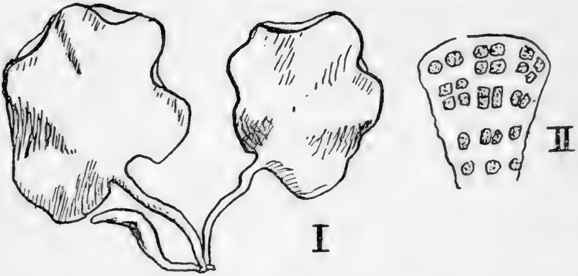

Fig. 4.—*Prasiola stipitata.* I.—General appearance of plant magnified about four times. II.—Portion of frond magnified 300. The living cell contents are embedded in the flattened jelly which originates by the swelling and growth of the cell walls.

not motile, and the plant is furthermore increased by budding and by outgrowths from detached portions of thallus. The cells are very regularly arrayed in the thallus, and the conformation of the plant is clearly the result of a co-ordination existing between the constituent cells, and this is of a tolerably advanced nature. Indiscriminate multiplications of the individual cells has been replaced by a more ordered and regulated distribution of the power of division amongst the cells which together make up the Prasiola plant. The relation of the frond to light is one of the important factors in bringing this about. But there is, besides this, and perhaps behind it, a subtle intercommunicating influence between the individual cells which together constitute the colony, and this influence determines the share that each is to take in the building up of the organism as a whole. Although we may find it impossible to identify the exact nature of this influence in the majority of instances, we know quite enough to convince us that it is of a material nature. We are well aware that the processes of growth, and many other bodily functions besides, are greatly affected by the presence of even minute traces of certain substances, and the physical approximation of the cells of an organism renders it possible for substances to diffuse from one to the other, and thus to determine, in a plus or minus direction, the rate of cell growth and multiplication.

# CHAPTER IV

## THE CELLS AND THE ORGANISM

Turning from the flattened forms to the filamentous types of algæ, we find a great variety of forms, accompanied by a very different degree of autonomy in the constituent cells of the filamentous body. Moreover, we see very clearly that closely analogous forms have been reached by several evolutionary routes. In other words, much the same kind of organisation may have been arrived at by plants which have descended from several diverse simple stocks. This convergence of type, or analogous similarity between remotely related forms, is of fairly wide occurrence both in animals and in plants, nor is it by any means restricted to the simpler members of either kingdom.

Our first illustration of an alga organised on the filamentous plan is afforded by the species known as *Hydrurus fœtidus* (Fig. 5). It is an aquatic plant, rare in Britain, but fairly abundant in many Alpine rills near the melting snow. The reason of this is that the alga only thrives at a low temperature, soon perishing in water above 12° C. (= about 54° F.). The plants are rather plumosely branched above, and the branchlets are

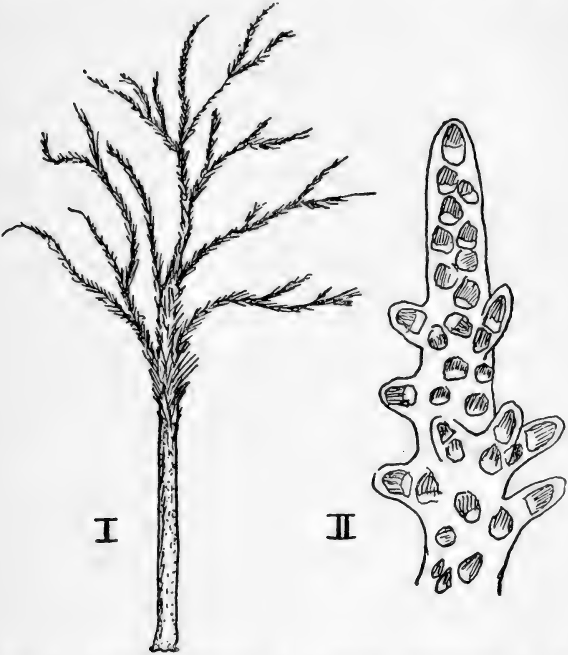

Fig. 5.—*Hydrurus fœtidus.* I.—General character of the plant. II.—One of the tips of the branches highly magnified showing the cells of which the plant is built up. The protoplasmic bodies are embedded in a common jelly formed by the swelling up of the walls or membranes, but the innermost layer forms a sharply defined skin round each protoplast.

“ hairy ” or villous. The lower part forms a smooth stalk, and is attached to stones, etc., by a slightly expanded disc-like foot.

An individual Hydrurus is made up of a colony of unicellular algæ, the walls of which have become swollen and rather firmly gelatinous. The whole organisation of the plant depends on the different mode of development followed by the various individual cells. The apices of all the branches and hair-like protuberances are occupied by single cells, and it is to these that the alga owes its definite form. The terminal cells of the branches multiply by dividing longitudinally; one of the two daughter cells then gradually slides in front of the other and continues to function as the growing apex, the other one, which has taken a rearward position, contributes to the building up of the plant body. Some of these cells behind the apex extend outwards from the cylindrical surface and become the starting-points of new branches; or, if their growth is but limited, they merely give rise to the villous hairy outgrowths.

The important lesson to be learned from Hydrurus is that a definite *co-ordination* exists amongst the individuals composing the colony or association. In this way it becomes possible to speak of the terminal cells as "apical cells"; that is to say, they have assumed the rôle of determining the fashion of the branching, the rest of the cells merely building up the plant on the lines laid down at these apices. Although Hydrurus recalls other algæ already described, in so far as it consists of an organised cell colony, it is very far removed from a near relationship with them, for it belongs to quite a distinct group. The cells are of a yellow colour, and when the protoplasts escape from their containing gelatinous walls they only possess one cilium instead of two as in Chlamydomonas.

The majority of the filamentous algæ are composed of cells of an elongated form, placed end to end, and the colonial origin of such plants is more and more obscured owing to the specialisation which takes place amongst the cells, for these gradually cease to form merely coherent but obviously distinct units. They come to exist as mere parts of a higher organisation, the latter more and more controlling the arrangement and development of the constituent cells. Thus the relative importance of the cell and the organism is gradually reversed. In the lower types it is not always easy to discover the organism in a congeries of cells, whilst in the higher ones the controlling organisation of the complex individual may almost completely override the independence of the constituent cells.

As an example of a plant the cells of which have still retained a considerable measure of autonomy, we may name Spirogyra, one of the commonest of the thread-like algæ to be met with in ponds and ditches, where it is easily recognised by its bright green colour and the slippery gelatinous character of its membranes. The cells of the filaments are commonly elongated, but each one behaves very much as an independent unit. The effect of one cell upon another is of the slightest under ordinary circumstances. Each divides transversely, and so multiplies, independently of its neighbours. The filament thus grows in length, but it usually has no distinguishable base or apex, nor does it branch. Altogether the organising effect of the cell union is as yet of the very simplest kind.

Another common alga, Cladophora, presents quite a different state of affairs (Fig. 6). This plant, like the foregoing, consists of cells placed end to end, but there the similarity ceases. Each cell is definitely part of the organism. The filament is attached by a specialised basal cell and it increases in length solely by transverse division of the apical cell. Branches may spring from the cells behind the apex, and they then commonly appear in regular sequence, the youngest branches arising as outgrowths from the anterior (*e. g.* nearer the growing point of the stem) end of the cell nearest the apex.

Not only, therefore, is the plant as a whole organised in such a way that there is a base, as distinct from an apex, but this distinction is also impressed on every cell[1] which helps

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[1] In a certain sense the expression "cell" is not appropriate to the structural unit of Cladophora, since each "cell" really represents a syncytium (p. 21) because its protoplasm contains several nuclei.

to make up the Cladophora plant. It may easily be shown that the co-ordination is a real one, and that it depends in some way on the mutual reactions between one cell and another, by means of an experiment on one of the marine species of the genus. If the plant be placed in sea-water to which a strong salt solution is slowly added (up to about 12·5 %), the protoplasm of each of the cells contracts away from the walls, and forms an ellipsoidal mass within each cell cavity. The protoplasts then surround themselves with new walls. After allowing them to

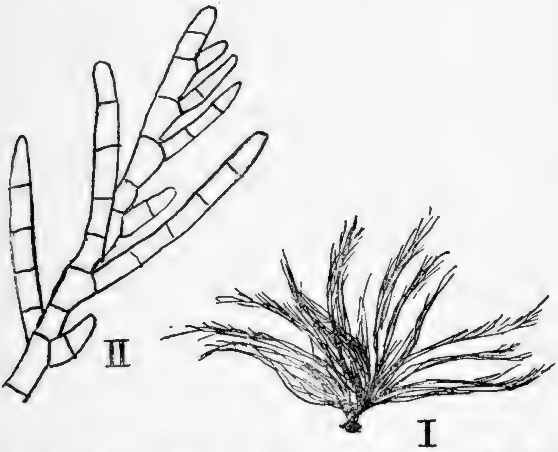


Fig. 6.—*Cladophora sp.* I.—General habit. II.—Magnified filament.

remain in this condition for about four days the strong salt solution is gradually replaced by sea-water. The ellipsoidal cells swell out until they approximately fill the space they previously occupied within the old membrane. But the disunion has obliterated the mutual relationship formerly existing between cell and cell. Each one proceeds to develop without any reference to the rest, and puts out a basal attaching organ below, which usually penetrates the adjacent cell cavity. Later on the cell also proceeds to grow in the apical direction. Thus the individual cells of the filamentous colony have been, in this experiment, released from the influence which bound them together into an organism, and have recovered complete autonomy and individuality. This has occurred as the result of sundering the protoplasts from all communication with one another for the period of time during which they remained contracted in the strong salt solution.

An experiment such as this is specially valuable, since it enables us to appreciate not only the reality of the continuous interchange of material between cells that are in close contact, whereby co-ordination is rendered possible, but it serves to show how closely this co-ordination to form an organism is bound up with such mutual interchange. For the protoplasts, although separated by membranous cell walls from each other, are yet in intimate connection; in many instances connecting strands of protoplasm have been demonstrated, and these serve as the obvious channels of direct communication between the living contents of adjacent cells. When the interchange has been sufficiently interrupted the old order cannot be again restored. The cells are released, as it were, from the influence that previously controlled them and caused them to be welded together into a higher individuality. Each cell, thus breaking away from the union, reverts to a more primitive condition, recovering an independence akin to, and perhaps identical with, that which distinguishes zoospores and other reproductive cells that are set free from the organism which gives them birth.

Although the simpler filamentous algæ, and especially the branching kinds, share with the primitive flattened leaf-like types the advantage of disposing their surfaces so as to make the most of the means of illumination, they yet remain far behind the more advanced types, in which other functions beside those of photosynthesis press for notice.

The larger seaweeds, although their green colour is masked by yellow or red pigment, are as dependent on light for the manufacture of their food as are their simpler green companions. But their *size* introduces an element of physiological complexity.

It will be remembered that it is only the directly illuminated cells which take an active share in photosynthesis. What is the use, then, of those vast numbers of internal cells which lie beneath the outer surface of a large seaweed, and constitute its main bulk? Let us examine one of the big seaweeds, for example Laminaria, which form the large leathery strap-like plants growing below the tide limits. We shall find it consists of a stout stalk, firmly adhering by a specialised base to the rocks, and thinning out abruptly above to form the flattened frond. The cells which compose the plant are by no means all alike, and at least three different kinds can be distinguished. First there are the crowded, rather small ones, forming the superficial layers. These are those chiefly concerned in photosynthesis. Beneath the outer layers are other cells, larger and more irregular in shape. These are, partly at least, concerned in storing up the surplus products of photosynthesis. Thirdly, in the more central regions of the massive stalk are to be found strands of very much elongated cells which clearly serve as *conducting elements.* In some of the larger seaweeds the cross partition walls between these cells are visibly perforated, thus admitting of still easier passage of soluble contents along their course. Some of these large brown seaweeds recall the habit of our terrestrial plants in that they even throw off their " leafy " portions periodically, and produce new ones by the rapid division of the cells in the region between the stalk and the base of the expanded frond.

# CHAPTER V

## THE "NON-CELLULAR" TYPE OF ORGANISATION

In the series of plants hitherto considered we have been mainly concerned in tracing certain lines of evolution in form and structure, accompanied by a corresponding differentiation and specialisation, amongst the cells of which the bodies of the plants are constructed. These culminate in such forms as the higher red and brown seaweeds in which the character of leafy plants is very closely imitated, save in one important respect. The terrestrial plant, unlike the submerged seaweed, is exposed to difficulties connected with the *water supply*, and, as we shall subsequently see, this has necessitated structural and other developments far in advance of those exhibited by aquatic plants. Indeed, a high degree of cellular differentiation is really not essential for water plants, and we shall find that the complex structure of terrestrial species becomes simplified in any descendants that may have taken to a watery habitat.

Even amongst the algæ high differentiation of external form is not *necessarily* associated with a cellular complexity of corresponding magnitude. This is well seen in those seaweeds that consist of a large number of cells which, though enclosed in a common peripheral membrane of cellulose, are not partitioned off from each other by cell walls. An example of such a plant, which combines a somewhat highly differentiated external form with an internal structure of remarkable

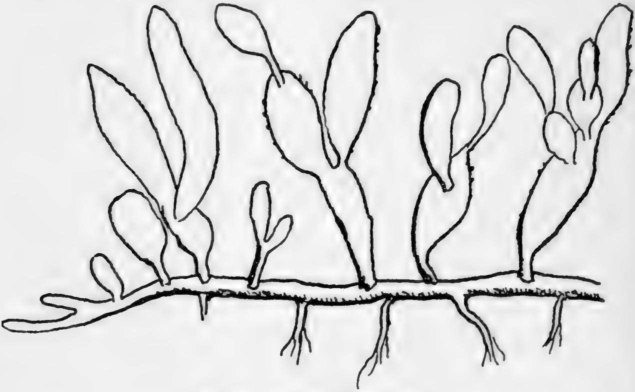


Fig. 7.—*Caulerpa Stahlii.*

simplicity, is furnished by the seaweed known as *Caulerpa Stahlii.* As is shown by the annexed illustration, the plant consists of a creeping stem from which arise the erect leafy expansions; while the whole is anchored by root-like structures which penetrate, or adhere to, the substratum. In spite of this high degree of external differentiation, there is no internal partitioning, and no one of the vast number of nucleated protoplasts, which together make up the living substance, is segregated physically from its neighbours by obvious boundaries. But there is one significant and interesting feature about the distribution of the nuclei in the protoplasm. They are crowded at the growing points, and are more widely spaced asunder in the older regions. In this apparently trivial circumstance we can discern exactly the same arrangement as would have been observed had the partitioning walls been actually present, for the dividing cells in the growing points always appear to be both numerous and small, owing, of course, to the rapid cell division which is going on in such regions.

Now this "non-cellular" or "syncytial" (see p. 21) type of organisation entails certain obvious disadvantages on its possessor, but we find that in some instances the attendant risks have been overcome in a wonderful way. On coral reefs and similar calcareous stations an alga known as *Halimeda Opuntia* is sometimes found (Fig. 8). It resembles in its general shape a small Prickly Pear

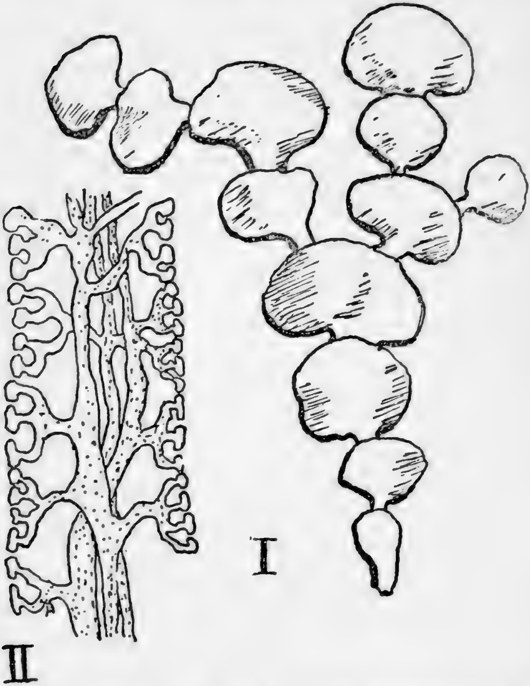


Fig. 8.—*Halimeda Opuntia.* I.—General appearance of the plant. II.—A section through one of the flattened lobes to show the palisade-like peripheral branches passing into the broader longitudinal filaments or strands.

or Opuntia. From an attaching organ there rises a jointed and much-branched plant.

The whole is strongly impregnated with a deposit of lime, whereby the plant acquires a considerable degree of strength and rigidity. The remarkable cactus- or opuntia-like form is produced by a wonderful weaving together of the branching filaments of which the whole plant is made up. There are no traces of cross walls in these tubular branches, but there is a considerable difference between the different regions of the branches themselves. The lower part of each branch system runs down the centre of the plant, while the final short twigs form the outer surface of the flattened segments. These final branchlets are closely adherent, and the flattened segment of the plant, looked at from the outside, seems to be clothed with a mosaic of small cells—these being, of course, the tips of the branches just mentioned. Not only this, but the chlorophyll is almost entirely confined to these peripheral branchlets, whilst the hinder and wider parts of the tubes serve to store and distribute the food material manufactured in the tips when exposed to light.

Halimeda, then, furnishes a wonderful example of co-ordinated growth. The singular completeness with which it has solved the problem of attaining a very high degree of specialisation with the simplest materials, extends to every detail of its structure. It is admirably adapted, both to utilise the light and to store away the material products of photosynthesis; whilst it has overcome the disabilities apparently inherent in its type of organisation, by strengthening and cementing together the branching filaments, of which it is built up, by means of the calcium carbonate which it withdraws from the sea-water.

The consideration of the noncellular or syncytial plant has been introduced in order to illustrate the varieties of one possible type of structure. Save, however, for the production of a few aquatic representatives it does not mark a line of important advance. The multicellular condition contained within itself the promise of the future, and it is as multicellular organisms that the higher plants have been evolved.

It will be useful at this point to sum up the salient points of the preceding discussion, so as to gain a clear starting-point from which to study the evolution and modification of form and structure in the higher terrestrial forms of life.

We have seen the striking consequences which accrue from the possession of an investing membrane in their effects upon the mode of nutrition, and indirectly upon other functions, *e. g.* that of motility, in plants. We have learnt in the relatively lowly members of the vegetable kingdom which have been passed under review, why a need for the presentation of the green surfaces to light should be a matter of such cardinal importance as to dominate the organisation of every one of them. We have also followed out the gradual loss of motility, and the coherence of the individual cells, for a period of their lives at any rate. We have furthermore recognised the fact that there exists a mutual influence, of a material kind, which leads to the co-ordination of the cells of a colony in such a way as to produce, not a mere congeries of separate entities, but an organism. In other words, we have traced the gradual curtailment of the individuality characteristic of the primitive cells, and have witnessed the corresponding transference of it to the cell colony as a whole. This transference of individuality is intimately connected with physiological correlation, which is doubtless exerted through functional and material agencies—largely by modifications in the nutritive processes—with the result that each cell unit is intimately affected by what is going on in its neighbours, as well as in other and more remote regions of the organism; the final result is that the cell tends to become more definite and circumscribed in form, and more limited and specialised in function. To put it a little differently, the efficiency of the colonial organism is purchased at the price of the individual independence of the units which compose it.

If, however, we ask the question, What *advantage* do the cells gain by this union? the answer is not easy to give. The unicellular forms succeed very well, and they live in the same sort of environment as the multicellular colonies. This proves at once that each is suited for existence, in so far as physical conditions are concerned. We may indeed inquire whether the more specialised colonies actually do succeed better at all than their simpler unicellular relatives. In the higher forms there is the accumulation of food-supplies, and such consequent advantages as accrue from the possession of these reserves, but it is clearly impossible to see how this could account for the *origin* of the multicellular types. Perhaps, indeed, we are attacking the problem at the wrong end by regarding it as one of profit and loss at all. It seems at least as likely that the same sort of influence which we discern to subsist between, and to determine the organisation of the units of a specialised colony, operates in a similar, albeit in a simpler and cruder, way between the potentially free units of a primitive colony. In other words, the cause of coherence is primarily independent of advantage or disadvantage, and may hardly exceed an almost accidental lack of disunion (*e. g.* in Spirogyra); or it may depend upon some attractive influence which causes the units, primarily separate, to cohere in clusters, as happens in the series of algæ exemplified by well-known forms such as Volvox or Hydrodictyon.

# CHAPTER VI

## THE GREEN LEAF

We now pass from the study of the lower types of green plants to a consideration of the higher and more specialised forms of terrestrial vegetation. But if we restrict ourselves to a comparison of the vegetative organs of the more highly differentiated algæ and of the higher plants, we shall be struck, not so much by the dissimilarities, as by the likenesses which exist between them. We meet with the same specialisation of the shoot into a stem bearing thin expanded structures—the leaves. There are the same organs for attaching the plant to rough surfaces, or anchoring it in a looser sub-stratum. It is not difficult to discern in the influence of light the common factor which has been chiefly concerned in the production of these resemblances, so far at least as external form is concerned.

But when we probe more deeply into the matter the real differences between the two classes of plants begin to make themselves apparent. They consist, so far as the vegetative structure is concerned, in a specialisation of cells on the part of the land plant which may reach a grade of complexity almost infinitely beyond that to be encountered in any alga. Furthermore, the organs of attachment in the land plant no longer serve merely as "holdfasts," but they discharge important functions in connection with the absorption of water and mineral food-supplies. Their structure becomes increasingly modified with reference to the larger functions they have to discharge.

In another respect, also, the higher plants differ from the lower, namely in the greater degree of definiteness with which their various organs are produced. In other words, the *organisation* of the individual is as a whole more specialised, and is less apt than are simpler types to vary its normal sequences of growth. The different morphological structures are less and less susceptible of alteration than is the case with more primitive plants, in which the bonds of correlation and co-ordination between the constituent cells and tissues are weaker.

If we ask why there should be this advanced degree of anatomical differentiation associated with a land habitat, we shall find the answer to lie on the one hand chiefly in the needs for adequate water supply and all that this involves, and on the other in the demand for a body constructed on sound mechanical principles, so that it may be enabled successfully to withstand the various stresses and strains to which it is continually liable to be subjected.

Neither of these needs is specially pressing in the case of water plants, and indeed we find that when any of the descendants of the land flora take to an aquatic life, they tend more or less rapidly to lose those distinctive anatomical characters that marked their terrestrial forebears. Plants which are growing submerged in water are obviously better fitted to absorb it through any part of their surface and consequently have less need for elaborately specialised organs, either for absorption or conduction, than those whose roots alone are in contact with the damp soil, while the rest of the body is exposed to the drying influence of currents of air.

At the same time the water plants also escape most of the mechanical difficulties, and easily maintain a properly spread out leaf surface, and even an upright position, owing to the circumstance that their specific gravity is so nearly identical with that of water. Their weight thus becomes an almost negligible factor, especially as they are often buoyed up in the water, owing to the presence of air or gases entangled in their tissues.

But most of the higher water plants have not entirely lost the traces of their terrestrial inheritance. Even the roots of many of them still function as absorbing organs, and the mechanical tissue is often present, though in a more or less rudimentary condition. Sometimes, indeed, as in species that inhabit swiftly flowing streams, the roots may exhibit new and remarkable developments that especially fit their possessors to occupy such stations.

Let us inquire somewhat more closely as to what are the special qualities, both of general behaviour and anatomical structure, which render a terrestrial life possible for plants. If we select a concrete example of a land plant, such as an oak tree, we observe that there is a large branching top, covered with leaves for part of the year. Below, this crown passes into the trunk, and the latter again ends in the branched root system underground. The leaves are, of course, the factories in which the operation of food-making is going on so long as they are exposed to the light. The roots are absorbing water from the soil, and such salts as are dissolved in it, whilst the trunk forms an intermediate conducting region through which exchange between the substances in the root and the rest of the tree can take place. The circulation of materials in a plant is not really like the circulation of the blood in animals, although an analogy—largely a false one—is often drawn between them, for there is no continuous circulating system in the oak tree at all comparable with the arteries and veins of the animal body. Nevertheless there is a process of exchange, though arranged on different lines, and serving quite different ends. In order to grasp this clearly, it will be convenient in the first place to cast a brief glance at the functions of the leaf.

The leaf absorbs from the air chiefly oxygen and carbon dioxide. The latter gas is present in very small quantities only, say about 2·5 to 3 parts in 10,000. Yet this carbon dioxide represents the sole source of the carbon which forms so large a part of the dry weight of the tree. Free oxygen is required, as it is by almost all living beings, for purposes of respiration; that is to say for the purpose of oxidising certain chemical substances within

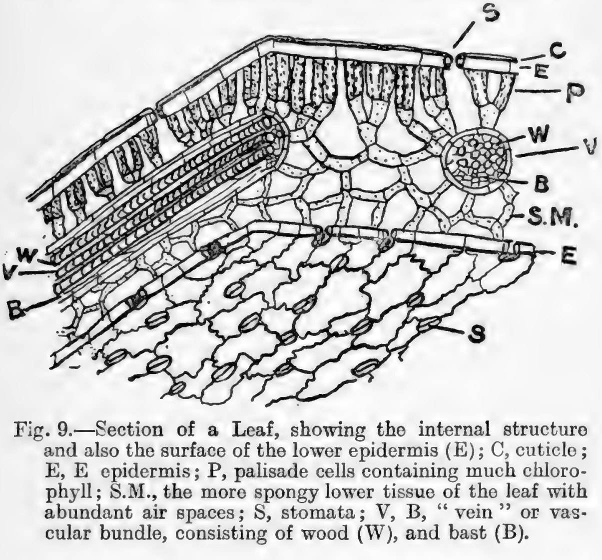


Fig. 9.—Section of a Leaf, showing the internal structure and also the surface of the lower epidermis (E); C, cuticle; E, E epidermis; P, palisade cells containing much chlorophyll; S.M., the more spongy lower tissue of the leaf with abundant air spaces; S, stomata; V, B, "vein" or vascular bundle, consisting of wood (W), and bast (B).

the cells. This property of respiration secures, *inter alia*, an economic transformation of energy within the organism.

In respect, then, of the functions of respiration and photosynthesis an oak leaf does not primarily differ, in essential respects, from a seaweed. But in the important matter of water relations the two are on a very different footing. It has already been pointed out that a supply of water to the living cells is essential for the exercise of their functions. The alga, in its watery habitat, has no difficulty in this respect, but the oak leaf, so far from obtaining, is continually losing water from its surfaces. Even in wet weather very little, if any, of the rain which falls on it is absorbed by the cells. This is owing to the circumstance that the outer layer of the wall of the external sheet of cells (epidermis) has undergone a change, and no longer consists of cellulose, through which water can readily pass. It has become converted into *cuticle*, which is extremely impervious to water, and partially so to gases as well. This cuticle is of extreme importance to terrestrial plants, inasmuch as it provides one of the chief means for preventing their losing water by the ordinary process of evaporation. All the water required by the leaf is received from the root by way of the stem, and it is distributed to all parts of the leaf by means of the *vascular bundles*, which are often known as the "veins" of the leaf. It is these "veins" which are left, and constitute the delicate network of "skeleton leaves" on macerating leaves in water. The vascular bundles are rather complicated in structure, and they represent the most highly specialised tissues of the plant body. A vascular bundle consists of wood (xylem) and bast (phloëm), and a thin band of tissue known as cambium often lies between them. They anastomose freely in the oak leaf, and in the stalk they are collected into a few large vascular strands which join the vascular tissues of the stem. Similarly the root possesses vascular strands, and these are likewise joined with those of the stem or trunk, and thus there is a general continuity of the vascular tissue throughout the plant. The water enters the root from the soil, passes up the trunk, and flows thence into the leaves, travelling through certain specialised cell elements of the wood. In the leaf it is distributed to various kinds of cells, and especially to those containing the bulk of the chlorophyll (P, in Fig. 9) in which photosynthesis is especially active. The greater part of it evaporates from the cells into the large air spaces which are present in the leaf substance, and the contained air is thus saturated with aqueous vapour.

The cuticle, which forms the outermost membrane of the epidermis, would prevent the exit of any water, either as liquid or vapour, if it were perfectly continuous. In the same way it would preclude the entrance of oxygen and carbon dioxide, at any rate in sufficient quantity. But as a matter of fact it is not continuous. There are immense numbers of minute gaps in the epidermis, termed stomata (Fig. 9, S), and these form the external orifices of an extensive system of air spaces which are present between the cells of which the leaf is composed. These intercellular spaces are of the utmost importance to the leaf, inasmuch as it is by means of them that gaseous exchange between the cells and the atmosphere is rendered possible.

Each pore or stoma is really a slit formed between two sausage-shaped cells of the epidermis, and these two guard cells, as they are called, can change their shape according as they become more or less distended with water. When they are distended, or *turgid*, the aperture between them becomes wider, as they lose water the pore tends to close. We see then that the leaf, as regards water, is a beautifully self-regulated mechanism. When a plentiful supply is available the opening of the stomata enables the vapour which saturates the air in the intercellular spaces to diffuse out; but when the supplies fall short the loss is avoided by the closing together of the guard cells. Other things being equal, it is advantageous that water should be abundantly available, as in this way mineral salts are brought to the leaves. A relatively rapid flow to these organs, however, only takes place when the surplus vapour is constantly passing away through the stomata.

But the stomata are important as the means of gaseous intake, as well as for the output of water vapour and other gases. Now, although the apertures are very numerous, the total sum of their areas reckoned as a fraction of the surface of the leaf is still very small. The amount of carbon dioxide in the air is likewise very minute, and yet the intake of carbon dioxide is very large. For many years the explanation of this apparent anomaly remained obscure, but investigations revealed the fact that the leaf actually absorbs as much carbon dioxide as if its chlorophyll-containing cells were exposed freely to air, and were not covered by a membrane or epidermis at all. The explanation is to be found in a remarkable modification of the ordinary conditions of diffusion through their perforated membranes. It is to the effect that when the orifices become small enough the rate of diffusion through them increases, area for area, up to certain limits. Or to express it more precisely; while the rate for relatively large holes varies very nearly as the *areas* of the holes, it varies as the *diameters* of small holes if these are sufficiently spaced apart.

In these respects, then, the leaf is an organ admirably adapted for the discharge, in the most efficient manner possible, of the important function of photosynthesis. The necessary passage of gases and water vapour, whether into or out of its interior, is achieved as the result of a nice adjustment to the physical conditions that regulate the diffusion of gases through a perforate membrane. If we try to explain to ourselves how such a mechanism could have become so perfectly evolved, how the correlation between the cells of the epidermal tissue became so perfectly —and apparently so purposefully—arranged and adjusted, we shall find ourselves confronted with a task of no mean order. And the same difficulty arises whenever we attempt to give a satisfactory explanation of any other instance of complex adaptedness in the structure of living things.

Utilising the physical advantages which the arrangement of its constituent cells and tissues have placed at its disposal, the oak leaf, under the influence of light from the sun, of carbon dioxide from the air, and of water from the soil, carries on the operation of photosynthesis in certain cells which are situated just beneath the epidermis. From their form these are commonly known as "palisade cells," and they are continuously active, provided the general conditions, such as suitable temperature, light, and adequate supplies of oxygen and of carbon dioxide, are fulfilled. The need of oxygen by plants, in contrast to animals, is a very modest one, and indeed the oxygen which is liberated within the leaf during the process of photosynthesis may really suffice for respiratory purposes. Sugar then begins to form in the manufacturing cells. But it is a characteristic feature of this, as of so many other chemical reactions, whether in the living cell or in a test-tube, that the rate of formation of the soluble product slows down as the concentration of that product increases. Any such wasteful lowering of the rate of production is avoided in the plant cell by the starting of a second process, whereby insoluble starch is formed as soon as the concentration of the sugar in the cell reaches a certain point. The sugar is thus continually prevented from accumulating in quantities sufficient to bring about the cessation of photosynthetic activity within the cell.

As long as the leaf remains attached to the tree, a certain amount of the sugar is, in any event, being withdrawn from the cells in which it is being manufactured. This sugar does not, however, diffuse from cell to cell in any casual direction. Thus it does not readily pass from one palisade cell to its adjacent neighbour. But it does very readily pass into the *subjacent* cells, and through them to the vascular strands of the leaf. These strands consist, as already explained, of wood and bast (or xylem and phloëm) and it is mainly through the cells of the latter that the sugar travels, diffusing from one cell to another. The cells of the phloëm are of various shapes, but they are mostly elongated in the direction of the strand, and some have the transverse walls which separate the elongated cells of a row perforated by small pores. These are the sieve tubes, and much of the various food substances which reach the vascular strands passes through them. But it is probable that such an easily diffusible substance as sugar passes as well through tracts of other elongated, but not so obviously perforated, cells of the phloëm. Be this as it may, it is largely through the vascular strands that the sugars of the plant are carried away from the regions where they are present in excess to other regions where they are relatively deficient. This occurs whether the deficiency arises through the sugar being directly used up in the chemical operations of the cells, or whether the special conditions of the local deposition of food reserves are such as to produce a diffusion gradient, that is a steady flow *within the plant* from a place of high to one of lower concentration. It is well to emphasise the limitation thus expressed in the last sentence, for however readily substances may travel from one plant cell to another, it is a very different thing if one endeavours to get them to diffuse out of the region of the living cells into a mass of surrounding water, for example. Such attempts commonly do not succeed unless the cell protoplasm be first modified, as, for example, by means of an anæsthetic or by some more violent and lethal agent.

If a leaf which has been active enough to have accumulated starch in its tissues be examined after a sufficient interval during which photosynthesis has been in abeyance (owing to the absence of light, for example), the amount of starch will be found to be lessened, and it may have all disappeared. The reason of this lies in an extension of the process already sketched in outline. The sugar continues to be withdrawn from the leaf cell even after all further synthesis has ceased. But as the concentration of the sugar sinks, a ferment action makes itself felt within the cell. The starch is gradually attacked by a ferment or enzyme known as diastase, and it is thus converted into a soluble sugar called maltose; the maltose then continues to pass away from the cell, or at least so much of it as is not immediately required by the cell protoplasm itself. The process of migration continues till all the starch has been fermented and rendered soluble.

The change from starch to sugar is a very simple one, merely involving a dislocation of the larger molecular aggregate together with the incorporation of a molecule of water. It is of a totally different order of change to that which is involved in the *oxidation* of the carbohydrate. For oxidation involves a considerable change in the state of energy, as well as of chemical constitution.

The leaf starch, thus fermented into soluble and diffusible sugar, travels in the latter form to other parts of the plant. It passes to the growing regions, where it is utilised in growth processes, to storage tissues where it is reconverted into starch or into some other food reserve, or it is drawn towards any other centre of activity where a consumption of carbohydrate is in progress.

We have learned in a former chapter that water plays an important part in photosynthetic production of carbohydrate. It not only acts as a physical agent, by maintaining the protoplasm in that state of watery consistence essential to chemical change, but it also forms part of the raw material which enters into the actual composition of the sugars and similar substances. Furthermore it serves as the vehicle by which salts containing phosphorus, sulphur and other substances which enter into the composition of protoplasm, or are essential to its proper working, can enter the plant from without. The excess of water is eliminated from the plant by the diffusion or *transpiration* of the watery vapour through the stomata.

# CHAPTER VII

## ROOTS AND THEIR FUNCTIONS

In order to complete our story of the green leaf and its duties to the plant, we must know how the water is absorbed into the plant and how it is transmitted to the leaves or other organs where it is required.

We might still keep the oak tree before us as a concrete example in which to study these things, and we should discover that it is only by the *roots* that the tree obtains the water it needs, and that these organs absorb it directly from the soil in which the tree is growing.

If we attempted to pull the roots out of the ground it would be found that, even in a seedling tree, the task is not an easy one. They penetrate the soil deeply, and ramify widely through it. It is easier, therefore, and for certain other reasons better, to study the roots of a more easily accessible object—say a sunflower or any other herbaceous plant.

On carefully digging out the roots of such a plant, we should see that the tips are smooth and conical, a shape well suited to bore through the soil. At a short distance behind the tip, the root is rather velvety or hairy, and it is impossible completely to wash the soil away from this portion. Still further behind, the soil ceases to adhere to the surface. Other roots or rootlets are seen to be growing out, and still further away from the tip the diameter of the young root begins evidently to increase. Thus we distinguish four regions : (1) the tip and clean surface; (2) the hairy zone; (3) the region from which young rootlets are springing; (4) The older parts which are getting thicker.

The only part of the root which is actively absorbing water from the soil is the hairy zone, and the hairs themselves—outgrowths from the superficial cell layer—are the essential structures which perform this task. The apex is chiefly concerned with boring on through the soil, and it is covered with a characteristic covering of cells called the root-cap, the outer cells of which are continually being worn away by attrition in the soil, and as constantly being replaced by the formation of fresh layers from within. The superficial cells behind the region of the root-cap do not begin to elongate at once to form hairs. This does not happen till the part of the root from which they spring has ceased to elongate. The meaning of this at once becomes clear when we reflect that these delicate protuberances, the root-hairs, are in very intimate contact with the particles of soil—and if the part of the root which bears them were to continue to grow in length, they would be torn away from their attachment to the soil. They are only efficient so long as they are uninjured, and perhaps this helps to explain why the hairy zone is such a short one on any one root, for the hairs do not grow again when once they are injured or worn out. The underground system as a whole, however, repairs this defect by forming a mass of branching roots, each one of which may repeat the form and the four stages indicated above.

In order to understand how the root-hair, and the root as a whole, play their respective parts in the absorption of water, some acquaintance with the cellular structures concerned is necessary.

We can ascertain this by examining under the microscope sections of roots cut in various directions. The annexed illustration (Fig. 10) represents, rather diagrammatically, a transverse section of a root. The hairy outgrowths are the root-hairs. They consist of an outer cell wall enclosing the living protoplasm which lines the interior of the wall, though it does not fill the entire space, for its own interior is occupied by a "vacuole" of watery sap. Passing inwards from the superficial root-hair layer we notice a band of "cortical" cells consisting of several layers forming the rind. Still more interiorly we arrive at a starlike arrangement of certain cell groups. This inner cylinder is the vascular strand of the root, and it consists of wood (xylem) and bast (phloëm), just as in the strands of the leaf or

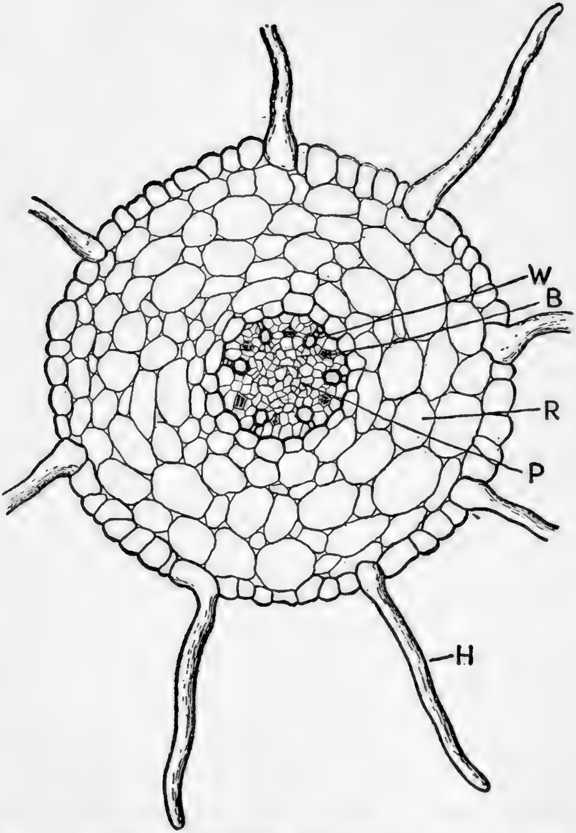


Fig. 10.—Root in transverse section. B, bast; P, pith; R, rind or cortex; W, wood; H, root hair.

stem. But in the young root the xylem and phloëm are arranged alternately, whilst in the stem and leaf they are superposed in pairs, with the phloëm usually exterior in position.

The cells of which the woody or xylem portion of the vascular strands is composed generally undergo a peculiar change in chemical and physical characters known as lignification. Lignified walls are less extensible and less collapsible, and in general are more rigid than the ordinary cellulose membranes. Moreover the lignified walls often become considerably thickened, which further emphasises the same qualities.

In dealing with wood, especially in the stem, we must remember that we are concerned with a complicated mass of tissues associated with the discharge of many and very different functions (Fig. 11). Some of the wood tissues are concerned with storage of food, others have to do with the mechanical functions of support, etc. To these we shall return later, but the special tissues of xylem that just now concern us are those which are connected with the conduction of water. The cells of the water-conducting tissue differ amongst themselves in details, but they are commonly elongated in form, and are arranged more or less in longitudinal continuity. It sometimes happens that the end walls separating two or more cells become perforated or even obliterated, so that the cavity of one cell becomes directly continuous with those of longitudinally adjacent cells. Such tubes, which have arisen by the disappearance of

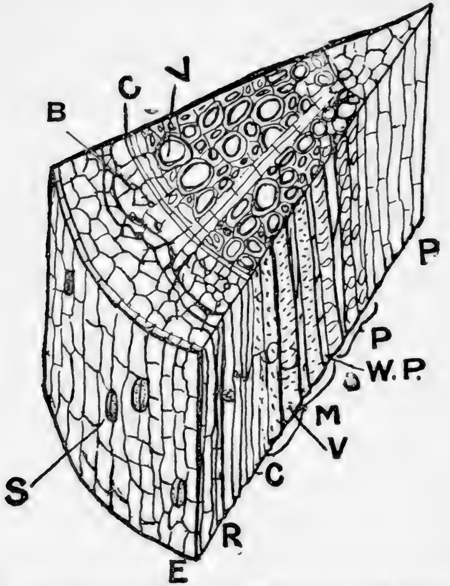


Fig. 11.—Diagrammatic section of young wood stem. B, B, bast; C, C, cambium; E, epidermis; M, later wood; P, the first wood formed (protoxylem); Pi, pith; R, rind; S, stoma; V, V, vessel; WP, wood parenchyma.

walls, are often called vessels. The water-conducting cells which keep their walls intact are termed tracheids. The tracheids and vessels then form the special tissues in the xylem which are concerned with translocation of water. The walls are thickened, but nearly always show thin spots or "pits." These are of special use inasmuch as the water from one tracheid can more easily and rapidly pass through a thin than a thick membrane. Now there are considerable variations of pressure conditions in these conducting channels, and an unprotected thin membrane would stand a good chance of becoming ruptured. The risk is obviated by a partial roofing over the thin spots by the thickened parts of the walls, which gives the pits a curious appearance under the microscope, and has caused them to be known generally as "bordered pits." Pits of this kind are, as we might now anticipate, of almost universal occurrence in water-conducting tissue. They are more easily seen in some woods than others, and perhaps in none better than in a bit of deal or pine wood (Fig. 12).

A striking character of these conducting tracheids and vessels lies in the absence of living protoplasm from them. All functional tracheids and vessels are therefore merely the dead skeletons of once living cells. The protoplasm disappears from them as soon as the thickening and lignification of the walls is complete. It is good that this should be so, for the presence of viscous protoplasm within the channels would greatly impede the flow of water through them.

In addition to the conducting tracheids and vessels, the wood always contains some comparatively undifferentiated tissue cells, such

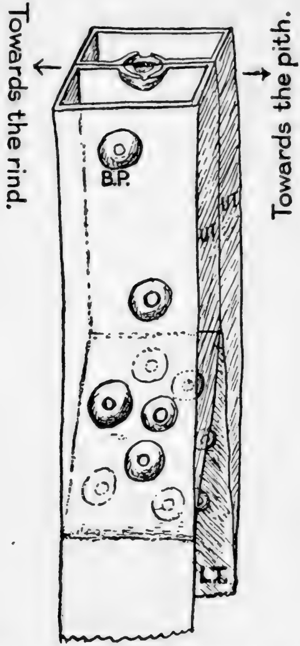


Fig. 12.—Diagram to show the bordered pits and how the tracheids in the wood of a pine are connected with each other. LT, lower tracheid; UT, UT, two upper tracheids; BP, bordered pits. At the top a bordered pit is shown in section (very highly magnified).

as are of common occurrence throughout the plant body; these, from their ordinary form, are generally called parenchymatous cells (Fig. 11, WP). The wood parenchyma, which largely serves the purpose of storage (or occasionally as an excretory tissue) is very often lignified. There are also other cells which are specialised for mechanical purposes. They are of various forms and sizes, and are grouped into more or less definite tissue systems. To the consideration of the latter we shall return when we come to consider the architecture and mechanics of the plant. For the present, however, we are only concerned with those tissues of the wood that are detailed for the service of translocation of water.

The vessels and tracheids form a *continuous communicating system* in the plant, and when water enters this system it can readily be transmitted from any one point to any other, the direction of flow being determined by purely physical conditions of pressure.

We can now endeavour to trace the passage of water from the soil into the water-conducting tissue of the plants, and thence into the leaves, to which most of the water that is absorbed ultimately finds its way. The root-hair is in close contact with the particles of soil, and it not only absorbs water from it, but it exerts a disintegrating influence on it owing to the excretion of carbonic acid from the living cell.

The absorption of water (which contains very small quantities of salts in solution) by the root-hairs is an active process, and it has to work in opposition to the surface-forces that tend to retain the water in the soil as a film which wets the minute particles of which soil is composed. The root-hairs are very closely adherent to some of these particles, and they wrest the water from the film which surrounds them. This disturbs the equilibrium of the water as distributed in the soil, and it causes a constant flow towards the spot whence it is being abstracted. It is to this circumstance that much of the drying effects of plants on soil is due, for the total amount of root-hair surface of a tree is far smaller than the area of ground that it will drain. Another example of the movements of water in soil is seen in the way that it loses moisture in dry weather. This is because evaporation is going on at the surface of the ground, and water is continually passing upwards from the lower levels to replace that which has passed into the atmosphere as vapour. The resistance to movements of water as the films lining the soil particles become very thin rapidly increases, and thus ordinary ground does not easily become dry for a great distance below the surface. Anything that disturbs the continuity of the soil particles also interposes a further hindrance to the movement of water, and this is why a garden soil that is kept stirred with a hoe withstands drought so much better than one that is not cultivated in this way. The particles of soil that have been stirred by the hoe are separated from each other, and thus the continuity of their surfaces with that of the lower soil is largely interrupted. At the same time the broken, loose soil serves to check evaporation, inasmuch as it shelters the lower unbroken (therefore continuous) soil both from the sun and from the drying influence of currents of air. It is a matter of common experience that if plants are grown in unwatered soil long enough, they begin to droop and wilt. This means that the root-hairs are not able to extract enough water from the ground to keep pace with that which is lost by the plant. Wilting takes place when the water contents of the soil fall below a certain amount, and this varies greatly in different soils, but is fairly constant for each particular kind. Thus, in sand a plant may utilise all the water down to about 1–2 %; while in heavy clay the water ceases to be available as soon as its content sinks below about 25 %. It is evident that there is probably some relation between the *physical* state of the soil, and its *physiologically* available water content. And this turns out to be the case. The fine particles of clay, with their relatively enormous surface, retain far more water than sand with its large particles and relatively small surface. Ingenious experiments on soil in centrifugal machines have shown that approximately the same amount of force is required to clear out water from clay so as to leave 25 % remaining as is required to leave about 1 % in coarse sand. These experiments are of great value in enabling us to see the way to attack many problems of plant and soil relations, and they show that the notion that the plant has forcibly to wrest the water from the soil is a fairly accurate one.

How, then, does the root-hair do this? What force can it exercise in the process?

Experiments show that a plant cell will, in general, absorb and retain water with considerable avidity. This it does by means of the so-called osmotic pressure exerted within it by various substances, such as sugar, organic acids, and the like, which are dissolved in the watery sap within the cell. For whereas water can pass freely in and out of the cell, the protoplasm either does not allow the dissolved substances to pass out, or it only lets them through very slowly. Without going at all fully into the difficult and complex subject of osmotic pressure in general, it may be remarked that, under these circumstances, water tends to flow into the cell and to such an extent that the cell sap exerts a very considerable pressure. This may easily reach a value equivalent to about eleven atmospheres. It is this circumstance which at least partly accounts for absorption of water from even relatively dry soil by the root-hairs, to make good that which is lost from other parts of the plant. For, as already explained, the parts of the plant above ground, and especially the leaves, are continually losing water through the stomata, and the water in the xylem conducting cells and vessels is being as continually drawn upon. Thus the whole water system is in a peculiar condition of considerable "tensile stress." This condition may be compared to a wire which is subjected to a powerful pull. This comparison may appear at first sight to be far fetched, but it really does illustrate fairly well what is going on, especially in the water conduits of tall trees. For when water is enclosed in suitable tubes (and the conducting tissues of the water conduits *are* suitable in this respect) the force required to break such a column of water is very great, many times that of the pressure of one atmosphere. As everybody knows, in an ordinary tube water can only be maintained at a height of about 32 feet by means of atmospheric pressure alone. But pure water, completely filling clean tubes of appropriate structure, will maintain itself at a height many times 32 feet, owing to its capacity of resisting tensile stress.

Although there are certain difficulties, all of which have not as yet been fully met, in explaining the movement of the current of water up through the trunks of tall trees, there is little doubt that the principle just indicated is the main factor in the matter, for though the column of water thus maintained is very stable as a whole, the individual molecules of the water are free to move within the column.

Of course, this condition of stress is propagated throughout the water system from the leaf back to the root. Water thus tends to be withdrawn from the outer cells of the root which abut on the ends of the conducting tissues within, and in this way a continuous flow is maintained from the root-hairs, which in their turn are replenished from the supplies of water contained in the soil. It comes to be a balance of forces represented on the one hand by those leading to the escape of water vapour from the leaf, and on the other the forces which tend to cause the water to be retained by the soil plus the effects of friction, etc., within the plant itself.

But, as a matter of fact, although the short description given above probably represents in a general way what goes on in connection with the translocation of water in a plant, there are other factors which are involved and may affect the process.

The living parenchymatous cells of the roots are not merely passive agents in the matter, for the water absorbed from the soil is in many plants (and perhaps in all) forcibly pressed or excreted from these living cells into the conducting channels. It is to this active propulsion of water within the plant that the phenomenon of " bleeding " is due. When trees are felled in spring, sap may continue for a long time to flow forcibly out from the surface of the wood. If vines are pruned too late the water thus pressed out by the root cells through the xylem will flow for many days, and it is squeezed out at a pressure often amounting to several atmospheres. The maintenance of the pressure depends on the living cells of the root, hence it is called "root pressure." Anything which interferes with the life of the root cells causes the pressure to diminish. Thus chilling the roots, depriving them of oxygen, or treating them with anæsthetics as well as with other poisons, may temporarily or permanently abolish root pressure.

No very satisfactory explanation has been given of root pressure, nor indeed of any other form of excretion. We are sure, however, that as our knowledge of the physical and chemical processes of protoplasm increases the difficulties will one day vanish. In the meantime the problems connected with water absorption and its movements within the plant are still in the interesting condition of incomplete solution. We know more or less *what* happens, but we do not as yet fully understand the *how* of the happening.

# CHAPTER VIII

## CORRELATION OF FUNCTION AND FORM

In the higher and more specialised green plants the organ principally charged with carrying on the important function of photosynthesis is commonly, though not invariably, the leaf. Now a green leaf only " pays its way " for so long as it is adequately exposed to light. But the intensity of light which produces the best results varies greatly with different plants. Moreover, a plant may lose so much water when exposed fully to the light, and hence to the air, that any advantage of illumination may be more than balanced by the chance of wilting. We find, as a matter of fact, that all these various considerations are of practical importance in the practice of forestry. Some kinds of trees will tolerate shade, others speedily succumb if they are not fully exposed to the light. Beech, for example, when young will thrive under the shade of the birch, and in many places it is best raised under this latter tree, which shields it in various ways during its infancy. But birch will not grow under beech. One is a strenuously light-demanding plant, while the other will readily tolerate shade.

This toleration only applies to the plant taken as a whole, and there are limits beyond which endurance of shade does not go. Most people who have wandered through a dense and well-tended wood must have been struck by the great difference between the forms of the individual trees which compose it and those of the same species grown in the open or in the hedgerow. The clean tall trunks and the compact small crown of the forest tree contrast strongly with the spreading growth of the park specimen. And yet the difference is merely a consequence of the different conditions of illumination. A tree grown in the open exposes its leaves to light on all sides. The spreading limbs space out the foliage and the leaves are all more or less actively functional. But closer inspection reveals the fact that it is only the leaves on the periphery of the tree and its branch systems which are thus flourishing. The inner portion is bare of leaves, or at any rate comparatively so. This is because the inner twigs which become shaded by the outer ones are starved, and sooner or later they die and fall off. The leaves they bore did not act efficiently, and they were quietly crushed out of existence.

Precisely the same thing, on a different scale, happens when young trees are grown close together, as in a well-managed forest.

The lateral branches, which in isolated trees spread out and constitute its charm, here compete with each other, and all are overshadowed by the topmost branches which alone get properly illuminated. Consequently the lower leaves become useless, and they, together with the branches which bear them, become starved and are destined to perish. The tops are constantly growing higher, while the trunk is as perpetually being denuded of its lower lateral branches. In this way the grand boles or trunks are formed which the woodman delights to see, and they are the distinguishing features of forests managed with skill and intelligence. The forester's aim is always secured, broadly speaking, in this way, though of course there are differences in actual treatment depending on the particular kind of tree or association of trees it is desired to produce. The tall trunks are the result of a sort of natural pruning, brought about by growing the trees at the correct distances apart, the actual distance being regulated by the size, age, and other conditions which affect the growth as a whole.

The amount of leaf surface is not only influenced by the available exposure to light, but is influenced by other conditions as well. Thus mechanical requirements need to be satisfied, and they may easily limit the dimensions practically attainable by the green surface as a whole. A leaf too weak in itself, or too feebly supported to retain a suitable position as regards the source of light, would be as useless as a heavily shaded one. Moreover, with the increase of the leaves the mechanical requirements vitally affect the whole subsidiary apparatus of the plant. The root is concerned in this no less than the stem, for the leaf depends for the proper discharge of its functions on an adequate degree of fixity on the part of the plant as a whole.

Another factor which materially influences the foliar organs of a plant, lies in the water supply, for if this be deficient or precarious, the leaf area must either be correspondingly reduced, or there must be found some means of checking the loss of water, or else the difficulty must be met in yet other ways. The particular form of solution of the water problem which happens to be adopted by any given plant is a matter that will mainly depend, as already pointed out, on its own inherent constitution.

It is worth while to endeavour to follow out some of the numerous and diverse ways by which those problems relating especially to mechanical needs and to water supply have been solved by various sorts of plants. Not only shall we encounter remarkable examples of adaptedness to special conditions, but we shall incidentally be brought into close contact with some of the more difficult questions of biological philosophy.

In any event we shall gain a clearer idea of the way in which the whole anatomical structure and indeed the whole conformation of the plant is dominated by the leaf or other equivalent green surface

# CHAPTER IX

## MECHANICAL PROBLEMS AND THEIR SOLUTIONS

We will, in the first place, direct our attention to the mechanical problems which affect plants. These are, broadly speaking, the same as those which confront the engineer in his ordinary work of building and construction. There are a variety of stresses and strains that have to be guarded against, unless the fabric is to collapse either by its own weight or by the action of other external forces. These mechanical requirements are satisfied in practice by choosing materials which, in the first place, possess the requisite physical characters of strength, toughness and the like; and in the second, by utilising them to the best mechanical advantage economy is combined with efficiency.

Now it may safely be said that in the

matter of engineering construction the plant has nothing to learn of man—although the converse might not be equally true. The more closely one examines the construction of a plant from the mechanical point of view, the more wonderful and complete does it appear. Certain cells or cell tissues become differentiated from their neighbours, and develop the requisite strength, elasticity, and other desirable qualities. They are not distributed in the plant at haphazard, but occur in situations where they are mechanically effective and physiologically appropriate. Furthermore, they are united so as to form definite tissue systems, and in connection with the more specialised types we may, without any exaggeration, speak of a *mechanical arrangement* of tissues.

Suitable rigidity is secured by the young undifferentiated parts of plants in the same way as in the more primitive ones, namely by the pressure of the watery sap contained within the cells. This confers the same sort of resilience as an inflated rubber ball possesses, and it amply suffices for many aquatic forms, although it is not sufficient for the needs of land plants generally, and only serves for small species growing under special conditions. An ordinary rooted plant has not only to hold itself in position, but it has to be capable of withstanding the effects of forces that are repeatedly acting upon it. Every time the wind blows, demands are made on the whole mechanical system of the plant. If it bends to the wind it ought

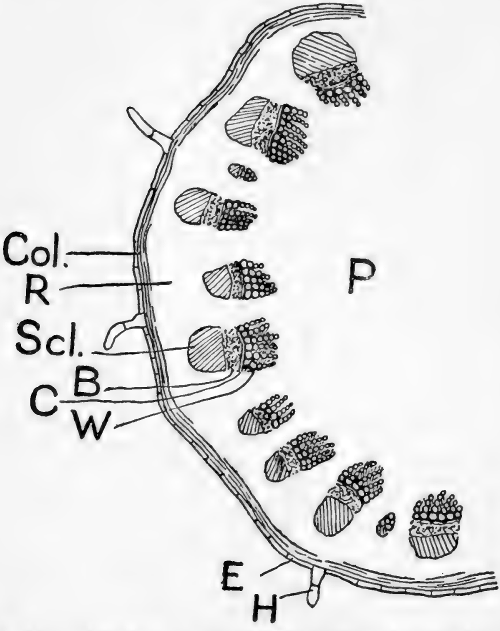


Fig. 13A.—Diagram of transverse section of part of a young stem of sunflower. B, bast; C, cambium; Col, collenchyma; E, epidermis; H, hair; P, pith; R, rind or cortex; Scl, sclerenchyma; W, wood.

to recover its old position when the blast is over. Its roots should be able to withstand the stress imposed on them, and prevent the tree from being pulled out of the ground or blown over, whilst its leaves must successfully resist tearing and the many other disruptive influences to which they are exposed.

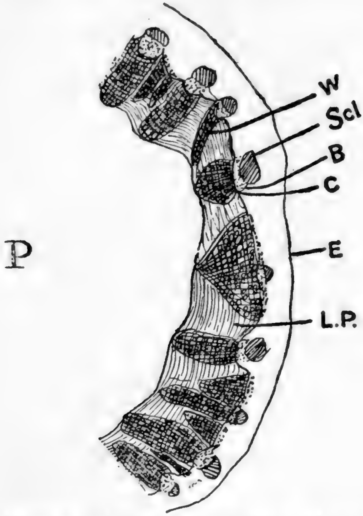


FIG. 13B.—Diagram of transverse section of part of an old stem of sunflower. C, cambium; E, epidermis; LP, hard lignified parenchyma; P, pith; Scl: sclerenchyma; W, wood.

An ordinary herbaceous stem, like that of a sunflower, affords an excellent illustration of the development of mechanical tissue and of its disposition so as to secure the maximum of efficiency with the least expenditure of material

(Figs. 13A and B). A fairly young stem cut across and examined under a moderate magnification shows that the centre is occupied by a bulky pith around which are seen the cut ends of the conducting strands—the vascular bundles. Just outside these are to be found the cut ends of small rod-like strands of tissue, the *sclerenchyma.* These run down the stem, following, roughly, the course of the vascular bundles. They are connected laterally at intervals, and especially at a node where a leaf springs from the stem. Each of these sclerenchymatous strands consists of very much elongated cells with pointed ends that grow and insert themselves between their neighbours above and below, thus giving the rod or strand of sclerenchyma as a whole a considerable degree of tenacity.

The walls of the cells become greatly thickened, and the rod is sharply marked off from the soft tissues of the rind in which it is embedded. Regarded from the point of view of its physical properties it exhibits remarkable strength. It is quite elastic even when submitted to considerable stress. This means that within certain limits it can be pulled out (*i. e.* elongated) by applying a force, and when this is withdrawn it will recover, and contract to its former length. In this respect the sclerenchymatous strands of many plants are but little inferior to good steel, and a strand one millimeter in cross section will stand a pull of about twenty kilograms, and still spring back when the weight is removed. They elongate more than a steel wire would do under the same stress, and they differ in another respect from steel, in that they break if loaded only a little beyond their elastic limits.

To understand how effective a system of such strands really is in enabling the stem to withstand bending stresses, or to recover its original position when the force (*e. g.* that of the wind) is withdrawn, we must consider the way in which they are arranged, and what actually happens when a stem is made to bend. In the first place the sclerenchymatous strands form a *tissue system*, and in the second place the strands cannot shift from their relative positions, being prevented from doing so by the surrounding cells of the stem which occupy the space between them. If we therefore consider the condition of two of these strands situated on, let us say, the east and west sides of the stem they may together be regarded as forming a girder, the relatively weak tissue of the stem lying in the east and west plane forming the " webbing " or latticework of the girder. Now when a girder of this construction is bent, the concave side is shortened or squeezed, while the convex side is lengthened or pulled. The intervening webbing merely serves to hold the two bars or flanges in their relative positions and is itself subject to less and less stress the nearer the middle line between the two flanges is reached.

Exactly the same happens in the plant. When a sunflower, or a wheat stem, is bent by the wind the tissue on the outer side is stretched, that on the concave side is compressed, and it is easy to see that both conditions tend to straighten the stem again. Since the axis of the stem is neither pulled nor compressed, it is obvious that there would be no advantage in placing the mechanical tissue where the pith is; the further away from the axis, *i. e.* the nearer to the circumference, the more effective it becomes.

But the wind does not act only in the east-west plane, and plants are apt to be subjected to stresses from any and all sides. Thus the girder systems are more complex in their arrangement, and are so multiplied as to be ready and meet the stress from whatever quarter it comes. Moreover, they commonly receive additional rigidity by being tied together, in a tangential direction as well as transversely, by specially strong tissues, at the nodes.

Now it is evident that this form of mechanical tissue is not suited for all the conditions that may be experienced by stems. For example, the young parts are often elongating, and sclerenchyma is far too little extensible to admit of this growth. On examining such a growing region we find that although the sclerenchyma strands are recognisable there, they are not yet functional. In fact the cells which compose them are only beginning to develop, the cell walls are still thin, the strand is itself still growing, and has not as yet developed those properties which will ultimately render it so valuable from the mechanical point of view.

But just beneath the outside skin or epidermis we may see that the cell layers which make up the periphery of the outer rind or cortex are characterised by cell walls of a remarkable form. They are much thickened, especially at the corners where the cells abut on each other, and this thickening often extends to the tangential walls, while the radial ones usually remain thin. The general impression they give is that of a number of concentrically arranged bands of thick substance (= the tangential walls) bound together by thin plates (= the radial walls). These thickened walls possess remarkable mechanical qualities which are very different from those which distinguish the sclerenchyma. They are much weaker, but this is partly compensated by their more advantageous position at the periphery of the stem. The essential feature in which they differ from sclerenchyma lies in the ease with which they can be stretched beyond the elastic limits, for a weight of about two kilograms suffices to produce a permanent elongation in a strand of one millimeter in cross section. They differ still further from sclerenchyma in that they do not break at this limit, but will stand a much stronger pull, by which they can be very greatly lengthened, although they become, of course, considerably thinner as the result. This tissue is often called *collenchyma*, from the peculiarly bright gelatinous appearance of the walls. It is specially adapted, by its extensibility, to the requirements of small and growing organs, whilst its inferior value as a supporting tissue is largely compensated by its advantageous position in the stem. Indeed, collenchyma affords a wonderful example of an accurate balance of qualities possessed by a tissue which is required to be carefully adjusted to meet very diverse needs. For whilst the function of support is its main *raison d'être*, it is obvious that it must not be so strong or so rigid as to materially interfere with the growth in length of the organ in which it is present.

It sometimes happens that the structures on which the rigidity of a stem depends have to be provided in a rather different way. In wheat, and most other grasses, the stem continues for some time to elongate just above the node or " knot." Most people know that it is easy to pull the stem out from the knot, and that the broken end is soft and succulent. But a series of such weak joints in a stem, however well the mechanical requirements might be fulfilled in the intervening regions, would of course be fatal to the retention of an erect position. In the grass this weakness is remedied by a curious arrangement of the leaf, which at first sight often seems to spring from the stem some distance above the node. In reality, however, the lower part of the leaf forms a cylindrical sheath surrounding and supporting the succulent, elongating portion of the stem just above the actual node. The cylindrical leaf sheath is supplied with abundant sclerenchyma, which is arranged in a more complex way than in the sunflower, but again in the strictest accordance with what we have discovered to be sound mechanical principles.

It is the mechanical tissue which forms the economically valuable fibre yielded by many plants—such as hemp, flax, jute and the like—and for commercial purposes it has to be separated by various processes from the softer tissues in which it lies imbedded.

As a plant becomes larger, the crushing effect of the increasing weight of the foliage and branches begins to make special demands for additional mechanical tissue. This is most often provided for by a large increase in the tissues of the wood. In a cross section of such a plant as an old sunflower the wood is seen to have assumed the form of a hollow cylinder, variously buttressed and thickened towards the pith.

In many of the perennial plants the character of the mechanical supporting tissue is less obvious, principally because it has to serve several purposes, and also because it is relatively so abundant that, if the expression may be allowed, it does not seem to matter much how it is disposed.

Every one must have noticed that the great majority of our shrubs and branching trees increase in girth as they get older. This increase is produced by a specially active layer of " embryonic " tissue known as cambium (Fig. 11c), which forms a cylindrical sheet of cells situated at the outer limit of the wood, which it thus completely encloses. By the active division of this cambium the cylinder or zone of young cell tissue is temporarily rendered thicker every year, and then the layers of cells which abut on the existing wood are themselves differentiated into xylem, to form the new annual ring of wood which is added every year to the wood of the trunk. A few of the outermost layers of the cylinder are similarly transformed into bast or phloëm, and only a thin cell layer now remains as a cylindrical sheet of cambium which still continues to separate the wood and bast. Next year this again increases in thickness, and the new layers thus produced go through the same changes as before.

In this way the annual rings of wood are produced which are seen when tree trunks are sawn across. It is due to the still undifferentiated and relatively thick sheet of young cells produced every spring that the " bark " is so easily separated from the wood at this season. For the walls are thin and the cells are rich in protoplasm and cell sap. They are thus easily ruptured, and every country boy knows that in late spring the bark of willow or ash twigs can easily be slipped off the wood as an unbroken cylinder. This is because the *débris* of the torn young cambial cells serve as a sort of lubricant which facilitates the process. Later on the bark will not slip off readily if at all, and this is due to the fact that the inner and outer cell layers of the previously undifferentiated zone have gradually become changed into wood and bast. The thin layer of residual cambium is now not thick enough, nor can it provide sufficient lubricant to enable the ring of bark to slip off.

The new wood thus produced consists of young water-conducting tracheids and vessels, as well as of other sorts of cells which have various functions to discharge. Some of these cells, as they change from the embryonic to the permanent or adult state not only thicken their walls, but grow considerably in length, inserting their tips between other similar cells above and below them. They are largely, though not exclusively, of *mechanical* significance. From a commercial point of view it is mainly to the mechanical tissue that woods of various sorts owe their technical value as timber.

A relatively considerable proportion of the new wood is thus more or less definitely differentiated to serve mechanical purposes. This applies to most of the cells which have thick and lignified walls, whether they are specifically mechanical, or are discharging other functions as well, such as that of storing supplies of food in the trunk. An enormous proportion of the wood of ordinary trees consists, then, of thick-walled cells of various kinds which are more or less intimately knit together, with the result that the whole possesses not only considerable strength but also a high degree of resilience. This latter quality differs greatly in different timbers, but it is entirely the result of the properties of the individual cell walls, combined with the manner in which the cells themselves have interdigitated with one another.

An ordinary tree, by virtue of these properties of the wood, is able to withstand the effects of a direct crushing stress far greater than it will ever be called to meet in nature. It has also, by virtue of its resiliency, the faculty of recovering its position when it is swayed or bent by the wind.

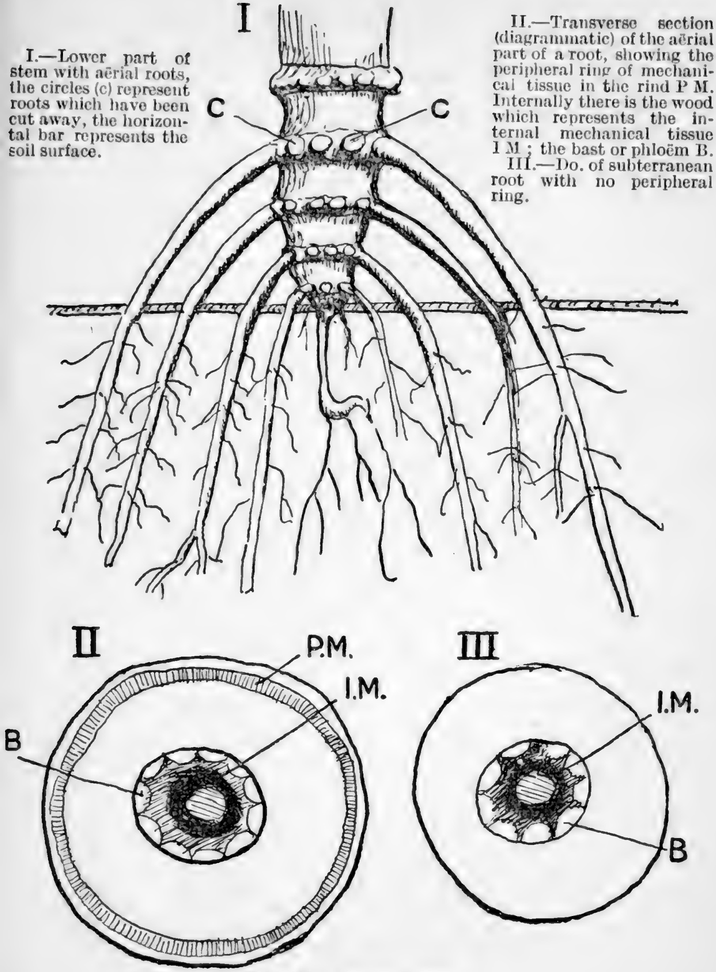
As regards the great lateral branches of large trees, their heavy weight of foliage and small branchlets renders the need for power of resistence and recovery from strains of various sorts even more pressing. Sometimes, indeed, they prove inadequate, as when a branch becomes overloaded with fruit. In the present year (1912) the great weight of beech mast is causing many large branches to bend down till they have come to rest upon the ground, and in not a few instances large arms of the trees have snapped, because the mechanical tissues have proved inadequate to meet the unusual demands thus thrown upon them.

When we compare the mechanical arrangements of the root system of a plant with those affecting its aerial portions, we are at once confronted by a new set of factors. There are two sets of conditions which largely control and limit the possible lines of variation in the mechanical structure of roots. One of these concerns the apical growth of the organ as it burrows through the soil, the other relates to the pull exerted on the root system by the swaying of the parts above ground when "they are fretten with the gusts of heaven."

As regards the growing points of the roots, the means for pushing forward in the soil is at the same time extremely simple and most effective. Unlike the stem, the actually elongating portion of the root is situated a very short distance behind the conical apex, and lies just in front of the zone of root-hairs already described (p. 73). The latter affords a sort of support which holds this part of the root immovable, whilst the turgid cells of the very short growing region, as they expand in growth, drive the smooth conical tip resistlessly forward. If the growing region were a long one, as it is in the stem, there would be an imminent risk of buckling, as may be easily understood if we consider what a thin, cord-like organ the ordinary young root is.

Farther back from the growing point the mechanical function of the root, as already stated, is that of holding the plant in the soil. The most effective position for the mechanical tissue to occupy to withstand pulls from various directions is along the centre or axis of the organ. For in this position the stress is most evenly distributed. Indeed, the mechanical strands may be regarded as cables in this form of construction.

Sometimes it happens that a root has to discharge still more complex mechanical functions, and its structure in this respect may then vary accordingly. The Indian corn plant, for example, has a thick stem, large leaves, and heavy fruit (Fig. 14). The rooting end where it penetrates the ground is quite thin, and the plant is obviously top-heavy, but a circle of roots springs from each of the nodes of the stem, that succeed each other at very short intervals just above the level of the ground, and each root grows towards the soil in a more or less arched manner; in this way the plant as a whole is well supported by means of a series of arched struts which admirably enable it to overcome the mechanical disadvantages of its original conformation. Now it is clear that when the plant is exposed to a force tending to bend it, the roots on the side towards which it inclines to fall over are exposed to crushing



I.—Lower part of stem with aërial roots, the circles (c) represent roots which have been cut away, the horizontal bar represents the soil surface.

II.—Transverse section (diagrammatic) of the aërial part of a root, showing the peripheral ring of mechanical tissue in the rind P M. Internally there is the wood which represents the internal mechanical tissue I M; the bast or phloëm B.

III.—Do. of subterranean root with no peripheral ring.

Fig. 14.—Indian corn.

or bending stress. An axial cord of mechanical tissue, however strong, would be useless to resist such a stress on the lee side, while the arched form of the roots would minimise the value of an axile strand of a root on the windward side. This special form of mechanical stress is overcome by the Indian corn roots in a remarkable way. The extra-terrestrial arched parts of the roots have a thick ring of mechanical tissue specially differentiated from the *cells of the outer rind*, whilst at the same time they retain the cord-like axile strand. Thus these roots are excellently adapted to withstand both crush- and pulling strains from whichever quarter they may come. Beneath the ground only the pulling strains, of course, are operative, and we find that the peripheral thick tissue ring is not formed in the subterranean parts of the root system.

# CHAPTER X

## SPECIAL FEATURES OF CLIMBING AND WATER PLANTS

There are several groups of plants in which the stems are more or less exposed to forces similar to those commonly affecting the roots we have been considering. We find that such stems often exhibit corresponding deviations from the normal stem structure, whereby they become enabled to withstand these special directions of stress.

One of the most interesting examples is furnished by the great group of climbing plants. The climbers have sprung from non-climbing ancestors, in the different ranks of the vegetable kingdom, but we here are concerned only with those which belong to the flowering plants. Many obvious points of close similarity are shared by all climbers, however distantly related they may be in other respects. They usually possess relatively thin main stems which are dependent on other objects, bushes, trees and the like, for their support. By growing to the tops of the latter they are enabled to expose their own abundant foliage freely to the light without the economic disadvantages attendant on the development of a correspondingly thick trunk.

But the various exigencies and risks inseparable from a climbing habit, have given free scope to the play of individual variation among the numerous species, both related and unrelated to each other, of which the great group of the climbers is composed. It is this circumstance that gives them their special interest, and also renders them so instructive.

Many of the climbers which grow in the tropical jungles exhibit extreme specialisation in connection with their climbing habits, by which they are enabled rapidly to reach the leafy canopy of the forest, although this is often many feet above the ground. Sometimes they steal a march on circumstances, as it were, and the seed is able to germinate in the upper fork of a tree. This occurs in many of the large figs, *e. g.* the India-rubber Fig, which, perhaps, can hardly be called a climber in the ordinary sense of the term. Plants of this kind produce roots which rapidly grow downwards and penetrate the soil, the young fig securing the great advantage that, when its foliage sprouts forth, it is very soon fully exposed to light.

Other climbers behave differently, and more nearly resemble the kind of growth of an ordinary plant, but with certain significant differences. The seed germinates on the ground, and the thin shoot, which grows upwards, along or through the supporting vegetation, only produces minute leaves, and at very distant intervals. It is not until the roof of the forest is reached that the large crop of big green leaves is unfolded, and their weight is entirely borne by the vegetation over which they are growing and spreading. Entangled as the climber becomes among the branches of the sustaining trees, it is evident that when the latter are swayed by the wind, the danger of snapping which confronts its thin stems is a very real one. Furthermore, while the plant is a young one, the risk of being parted from the root is not small. These difficulties are all obviated in several ways.

In many of them the first formed wood of the young plant consists almost entirely of strong mechanical tissue, and this is especially true of those climbers which produce no functional leaves worth mentioning till they reach the roof of the jungle. The presence of this axile cord of sclerenchymatous wood is most important to all these plants, for they need to be very flexible, and at the same time to be able to withstand very considerable pulls which might otherwise snap them asunder. The fact that they are admirably constructed in these respects is illustrated by the name of "jungle ropes," by which so many of them are commonly known—a popular tribute to their flexibility and their very great strength.

But it is evident that stems constructed on the lines just indicated have other functions besides purely mechanical ones, and these must be adequately discharged if the plant is to be a success. As soon as the foliage is produced, water is imperatively demanded, and thus there arises, so to speak, a conflict between opposing requirements. The sclerenchymatous tissue is excellent for supplying the needed strength, and its axile position renders it very effective. But it is of little or no use as water-conducting tissue. Now as a matter of fact we find that in the higher types of climbers (*e. g.* many members of the natural orders Leguminosæ, Sapindaceæ, Bignoniaceæ, etc.), that this strong flexible axile core is succeeded externally, and quite suddenly, by vessels of wide calibre which, though admirable as water conduits, are practically useless regarded from the standpoint of material strength. But the latter defect loses all significance as the plant grows older, for the difficulties that were to the fore in the climber's earlier life become obviated later on in a very simple manner. If one observes an old climber in the jungle, the lower part of the stem is often seen to be lying in snaky coils on the ground, and is evidently not at all exposed to any serious tractive forces. The peculiarity in question is due to the fact that up above, in the roof of the forest, the lower leafy branches of the climber are dying back as they give place to the younger ones springing nearer the growing points. Consequently the stem is gradually falling downwards as the older anchoring branches die and rot away. A further cause of the same slackening of the stem is to be discovered in some climbers, depending on the odd circumstance that the growth in length of the stem continues long after it would have ceased in ordinary plants.

The general effect of this elongation of the stem below the forest roof, in whatever way it is produced, is to relieve it entirely of all danger from tensile stress. Hence the stem can now, to the great advantage of the plant, become almost entirely concerned in providing the means for the transmission of water from the roots to the mass of foliage above. A secondary consequence also is to be seen in the development of the other tissues by which the food material manufactured by this foliage is distributed in the plant. If much of it is withdrawn to the roots the stem is rich in phloëm, but it is not especially so if, as is generally the case, most of the manufactured food is immediately utilised in the copious production of flowers and fruit.

The structure of such specialised climbers as these is capable of being interpreted as the result of a compromise, so to speak, between the opposing functions of nutrition and mechanics. The compromise is more obvious than in the majority of land plants because the issues are more strictly defined.

The narrow diameter of the stem is incompatible with waste or inefficiency in any of its parts, whilst by its unsuitability to act as an organ of storage, the obscuring effects of subsidiary functions are comparatively eliminated.

But there is always a danger in an appeal to metaphor, and the suggestion conveyed in the term compromise ought not to be accepted as containing any definite explanation of the facts, for it implicitly begs the whole question as to whether the plant *can adapt itself* to the exigencies of a particular environment; it rather indicates, without actually giving, an affirmative reply. But it may well be that the question is to be answered in a totally different way, and that what strikes us at first sight as an obvious "adaptation" may be still better described as an "adaptedness" brought about by causes and conditions not at all directly connected with the circumstances under which they are so clearly appropriate. In other words, the power of direct adaptation may be (and probably is) a very small part of the whole problem of the fitness so generally to be discerned between the plant (or animal) and its natural surroundings.

It is a remarkable circumstance that many of the climbers, especially the more advanced ones, exhibit a considerable degree of *anomalous* structure in their stems, and especially in their main stem. A large number of these anomalies are of obvious advantage to a climber, and are calculated to minimise risk of damage to the conducting channels of the stem under the special circumstances of their habit of life. The main stem is sometimes lobed, and it may ultimately even split into a rope-like mass of cordage. Or it may be flattened and wavy in contour, a character obviously associated with considerable resilience. Again, the soft phloëm is frequently embedded amongst the woody tissues, and is thus shielded from injury such as might arise through torsion of the stem, and in other ways.

But it is not true that every specialised climber is provided with a special or anomalous stem structure, nor are these abnormalities confined to climbing plants. The facts seem to indicate that the anomalies in question are to be regarded as instances of a break away from traditional structure, that they owe their origin primarily at least to the inner constitution of the living substance of the plants in which they arise. They may be regarded as one of the expressions of inherent tendency to vary which in dominant groups of plants is seen in a multiplication of related species. Any such break away from the type form of structure may prove useful in enabling a plant to develop new functions, or more perfectly to discharge nascent ones. And there are a very large number of instances, of the most varied

Fig. 15.—*Bauhinia anguina*, with special hooked branches which help the plant to climb.

kind, which indicate that when an organism has once modified its constitution so as to exhibit any special trend, the chances are all in favour of advance along the new lines, and very slightly indeed in favour of a return to the old ones. The history of abortion of parts (*e. g.* leaves), of concrescence in flowers, and many other morphological series of facts, may be adduced in support of this proposition.

Thus while stem anomaly is often (but far from invariably) associated with climbing habit, the connection is seen to be, after all, rather obscure. Sometimes perhaps fortuitous, at others it is to be regarded as the independent, but concomitant, and mutually advantageous result of a modification of the living substance of the plant itself. Finally, it is not unlikely that the abnormalities are sometimes elicited as the response, on the part of plants which have the faculty of making them at all, to stimuli given to the living cells by the strains and torsions, as well as by the internal nutritive conditions specially characteristic of the climber, or incident to the climbing habit.

The same sort of argument may be extended to apply to the well-known fact that in many climbers certain definite organs become modified, and are enabled thereby to attach the plant to a support. The particular organ (Figs. 15 and 16) affected varies widely in different plants, but whether it is a hook, a branch, a leaf, or part of a leaf, it is constant

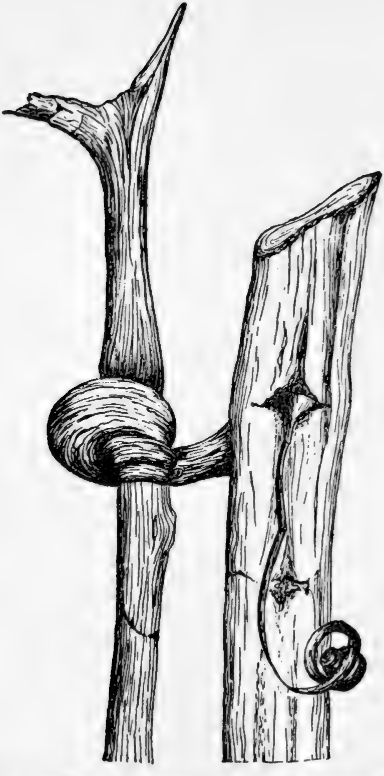


Fig. 16.—An old Bauhinia stem; one of the hooked branches, or tendrils, has grasped a support, while the other, which has not become functionally useful, has remained thin.

for the individual species. The most specialised of these organs are the tendrils.

Tendrils may be formed from specially modified branches as in the passion flower, or from leaf-stalks as in clematis, or from the leaves or leaflets as in various species of vetch, and even from roots as in the vanilla orchid. But they all tend to become very similar in form, and to assume in common just those characters that enable them so well to discharge their functions.

But the very fact of their diverse origin (from leaves, stems, etc.) in the different plants suffices to emphasise the importance of what we may call the internal living factor, as opposed to the environment directly, in their production. And this is further strengthened by the circumstance that they are produced fully formed, they are not gradually and tentatively produced and perfected during their development, any more than are any of the historically older organs of the plant. But nevertheless, many of them are endowed with the faculty of further growth in thickness and strength if they become functionally active. This power is not restricted to tendrils but is of widespread occurrence, and is especially obvious in the case of the stalks of heavy fruits. These, like functional tendrils, greatly increase the amount of mechanical tissue primarily present in their tissues as the fruits increase in weight. The advantage secured is in both examples the same, but the real causes responsible for its appearance are equally obscure. The most we can at present say is that in the exercise of the function new conditions are introduced which lead to the supply of abundant nutritive material, together with the power to use it. But the mode of interaction of all the inner functional conditions is far too complex for us to express the matter in any rough-and-ready formula. Least of all is it useful to say, in anthropomorphic fashion, that structural peculiarities like those of climbers are due to the plant having adapted itself to its environment. We readily discern that the plant *is* adapted, but we know remarkably little about the processes whereby this interrelation has been brought about. It conduces neither to clearness of judgment nor to the advance of science to mistake more or less fanciful descriptions for real explanations of complex phenomena.

Groups of plants such as climbers are interesting for the very reason that they serve to illustrate the fact that any species, whatever its ancestral origin, may join a specialised biological class provided it has the capacity for developing an appropriate structure. Another biological group is constituted by the higher water plants. These have, for the most part, descended from terrestrial forebears, and they display many significant features of interest in connection with their more recent environmental conditions. Some of them are still amphibious, and are able to respond to the stimulus of either land or watery surroundings by a suitable structure. For example, the common Moneywort

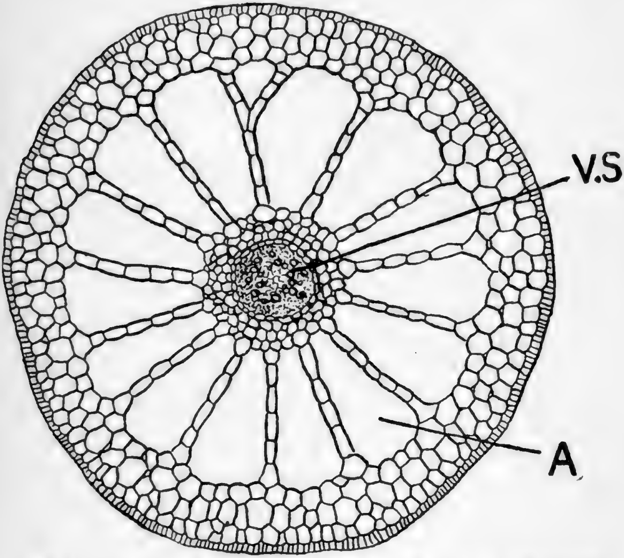


Fig. 17.—Stem of Water Milfoil (*Myriophyllum*) in transverse section. A, airspace; VS, vascular strand.

(*Lysimachia Nummularia*) of wet meadows will grow as an aquatic, a marsh plant, or as an inhabitant of dry soil. The reason of this is to be sought in the way in which the development of the cuticle is affected, though only indirectly, by the environment, whereby the loss of water is limited when the moneywort is flourishing in dry soil. Most plants do not share this faculty of quickly altering their chemical processes so as to become adapted to so wide a range of conditions.

The most striking character common to all the higher water plants consists in the enormous development of intercellular spaces (Fig. 17). These air-spaces, communicating finally with the atmosphere by the stomata, represent an exaggerated development of an aerating system that occurs in every land plant. The aquatics have not, in this respect, acquired anything new, they have merely enlarged and often specialised, what was already an ancestral trait. Such an aerating system sharply marks off the higher water plants from the lower ones. In the larger seaweeds it is true that there is often a localised formation of air cavities. These, however, serve rather as floating organs than for the general purposes of respiration and gaseous exchange generally.

The remarkable congeries of trees and shrubs that make up a mangrove swamp in the inlets and estuaries on tropical coasts furnish striking examples of specialised aerating systems. It is the roots which run through the mud of the swamp that are principally affected by the urgent need of free oxygen. After the root of a mangrove has grown for a certain distance, it bends up out of the mud into the air. Then as it grows on, it curls down and its tip again enters the mud. The bowed portion or "knee" which sticks up into the air forms a quantity of spongy tissue full of intercellular spaces, and as these communicate externally with the atmosphere, and internally with the intercellular spaces in the rest of the root, the respiration of the root cells is amply provided for, although there is no supply of free oxygen in the mud through which they grow.

A number of other trees of the mangrove swamp form special roots which grow up like spikes out of the mud. They do not again turn and grow downwards, but are definitely specialised as aerating organs. They may be compared to ventilating pipes, for their use is entirely confined to enabling an interchange to take place between the air in the plant and that of the atmosphere.

The submerged aquatic plants have to meet a set of conditions very different from those which confront the land vegetation. Inasmuch as they are surrounded with water there is no risk of desiccation, and the cuticle is poorly developed and often is hardly perceptible. Water is not continually being lost, nor is there any difficulty in obtaining it. Hence it is not surprising to find that the development of water-conducting elements is feeble. And one of the striking features of the water plants consists in the degenerate character of the wood. This poverty in water-conducting tissue is, however, chiefly to be seen in the parts which have elongated. The nodes, whence the leaves arise, often exhibit quite a considerable amount of vessels and tracheids. These parts of the stem, which do not elongate, are in sharp contrast to the internodes, in which practically all the growth in length of a stem takes place. In the internodes the wood is often merely rudimentary, and it may be absent altogether. On the other hand, the phloëm, in which the organic substances mainly travel, is usually as well developed as in a land plant, and sometimes even better, relatively speaking.

As regards the mechanical tissues, aquatics are specially interesting. They are almost of the same specific gravity as the water, and when the air-spaces are taken into account they are usually much lighter. Consequently, arrangements for providing the mechanical condition of support are unnecessary and would be wasteful. The only serious mechanical requirements are those adapted to prevent the plants growing in swift torrents being torn asunder by the force of the current. We find that, on the whole, the mechanical tissue, when present, and also the vascular strands, tend to occupy an axile position. This is especially advantageous for the latter, as the bending and waving movement of the flexible stems will naturally cause the minimum of distortion in vessels and cells which lie in the central region of the stem.

As far as aquatic plants are concerned, it is only for those which inhabit torrents that the mechanical tissue possesses much real significance. In the ordinary vegetation of ponds and sluggish rivers, a large number of the stems of the submerged vegetation are provided, it is true, with strands of mechanical tissue, but they often appear to be scattered rather at haphazard through the substance of the stem as a whole. Indeed, it almost seems as if these water plants had rather free play in the differentiation of the tissue in question. Ordinary aquatic conditions are not constant or strenuous enough to demand a high standard of mechanical efficiency. Hence the less rigorously adapted individuals are not eliminated, and the average of the race in this respect is soon correspondingly lowered.

We may complete our survey of mechanical tissues, and kindred matters, by briefly considering the mode of construction of the leaf from this point of view.

The flattened shape of most foliar organs evidently exposes them to risks of being torn, and furthermore it is of prime importance that the ordinary leaf should retain an extended form, and not easily buckle; otherwise the chlorophyll would cease to be advantageously displayed to light. The danger of buckling is partly met by the thickness and resilience of the epidermis, but much more effectively by the strengthening of the abundant "veins" or vascular bundles which run through it. These form, especially on the underside, a connected system of projecting and supporting strands.

In the elongated strap-shaped leaves of grasses, irises, palms, and suchlike plants, in which the principal veins pursue a longitudinal course in the leaf, we encounter the most beautiful examples of precise mechanical construction by which the proper form and position of the leaf is maintained, and is again recovered after any displacement that may have occurred. Bands of sclerenchyma run down the leaf, just below the upper and lower epidermis, and they are often placed, girder-wise, opposite one another, with the vein or vascular bundle running down between them. The latter thus occupies the position of the webbing of a girder. Although there is a good deal of difference in the details of different plants, the general application of sound mechanical principles of construction and arrangement, as well as the presence of suitable strengthening tissues, is patent to any observer who cares to examine the leaves.

The netted veined leaves of ordinary dicotyledons are exposed to considerable risks of damage by tearing the margins. The forms of many leaves seem at first sight almost to invite the risk of tearing, but any one who tries will soon convince himself that it is only an apparent, and not a real risk. The fact is, the veins form a beautiful system of unions or anastomoses, and these are often arranged in a series of arches which pass just under the indentations characteristic of the leaf margins of so many plants.

There are certain exceptions, however, to the general rule that leaf construction is adapted to prevent tearing. All palms have leaves which are primarily undivided. But by complicated processes which result in the dying out of strips of leaf tissue extending from the midrib to the margin, the leaf surface as a whole may be broken up into strips resembling pinnæ or leaflets. This occurs in the Coco-nut, and many other palms. These " leaflets " are very different from the true leaflets of a vetch and most other plants, where they arise as the result of a true process of branching. The so-called fan-leaved palms have leaves in which there is no great elongation of the " midrib," and the pleated or concertina-like folding represent the imperfect separation of the " leaflet " which is only completely carried out in forms like the Coco-nut, Areca, and other pinnate-leaved species.

The Banana plant is especially interesting in this connection, for it is provided by nature with a leaf quite unsuitable for a plant growing in any but the most sheltered situations. The banana plant consists of a thick herbaceous axis, sheathed by the bases of the huge leaves. The midrib of each leaf is a massive structure, and it possesses a considerable degree of rigidity. The blade, which it traverses, forms a long oval expansion, and thus exposes to the air a very considerable surface. Any one acquainted only with the banana as it grows in a plant house, where the air is always quiescent, might easily imagine that these large unbroken leaves must be remarkably well provided with mechanical tissue in order to maintain their outline intact. As a matter of fact, however, precisely the reverse is the case. The veins run out almost at right angles from the midrib to the margin, and anastomose very little with each other. There is thus no mechanical reason why the leaf should not be easily torn, and as a matter of fact this is what actually happens to a plant grown out of doors. The whole blade is reduced to a number of separate flaps or strips, each firmly attached, of course, to the midrib. Hence they can easily give to the breeze, and the banana escapes the overthrow to which it would be liable were it to hoist such large leaves, if unbreakable, in the teeth of the wind. The efficiency of the leaf surface is practically unimpaired by the tearing, because the vascular bundles, running parallel to each other, are not broken across, and their functions as conducting channels to and from the midrib to the green leaf surface are not interfered with in any way.

# CHAPTER XI

## ADAPTATION

The sketch of the formation and distribution of mechanical tissues attempted in the last few chapters, raises rather forcibly the question of how the existence and elaboration of the green leaf has succeeded in so profoundly affecting, even in this one particular, the construction of the whole organism. Of course, we recognise that the influence of the leaf depends on its position as the chief bearer of the chlorophyll of the plant, and to this extent our question becomes more precise. But if we limit ourselves for the moment to the consideration of this single problem of mechanical adaptation and correlation, in order to try to get a clear issue, we find that the issue is far from being clear, and the approaches to the problem itself bristle with difficulties.

It is true that we can readily find, in our analysis of the influence of the leaf, a very complete justification for the various mechanical adaptations and correlations which we have learnt to recognise. It is but one aspect of the much larger generalisation that there is a real and obvious relation between the structure of the organism and its environment. It is, further, almost a truism to remark that the more complex the organism the more patent is the perfection of its adjustment.

It is only when we get at closer quarters with our problem that its intricacies really begin to reveal themselves, and we are obliged to confess that our search for the causes, and even for the proximate agents by which the production of appropriate mechanical tissue is produced, has not been greatly rewarded. Of the means whereby the correlation is secured between functional need on the one hand, and its peculiarily correct satisfaction on the other, we have no positive knowledge at all.

It is easy to talk of "capacity to vary," "survival of the fittest," and so on. Such formulæ have their uses as expressing rather clearly certain definite facts, and as indicating in a general way some of the probable or possible processes which have been concerned in, or have at least influenced, the modification of plants and animals in their long course of evolution. But, after all, they are only generalised descriptions, and give us very little real or direct insight into the nature of the processes themselves, and yet it is precisely in the latter that the whole secrets of evolution, and all that it implies, are contained. In the particular example we have been considering, we want to know *how* the production of the mechanical tissue is effected, and *how* the remarkable and evident correspondence between its distribution within the plant and the various conditions imposed by the environment is brought about.

It might seem to be a simple affair to produce, or at least to promote, the development of mechanical tissue by merely subjecting a part of the plant to an artificial stress. But even if we could do this, it would still leave the kernel of the matter untouched. As a matter of fact, however, the attempt has often been made, but the results have been for the most part entirely negative. Vöchting, for example, endeavoured to induce the appropriate formation of strengthening tissue by attaching weights to plants in various ways, and in a number of different positions. In no single instance did he get a clearly positive result. But what cannot be done by merely applying an external force, can readily be accomplished if the requisite nutritive functions, and perhaps other internal processes also, become involved. We know how the growth of muscle is stimulated by use, consequent, at least in part, on the better nutrition which an improved condition of circulation ensures. An analogous instance is furnished by plants. Vöchting, experimenting with certain kinds of cabbages, found that after grafting heavy tops on to younger and thinner stems the latter forth-with began to differentiate mechanical tissue, appropriate both in form and position to the particular forces it became necessary to counteract.

In another connection, it may be observed that new *vascular* tissue can be differentiated in the leaves of some plants if their vascular bundles are injured, and this new tissue is formed at the expense of cells which hitherto have discharged other and very different functions. The union of appropriate tissues between stock and scion in grafting furnishes yet another example. These instances have been mentioned here to avoid giving too one-sided an impression of the evidence available in connection with the problem.

Such experiments as those above mentioned serve to throw a little light on the matter, by enabling us to realise that the final result is due not so much to a process of direct adaptation as to the interaction of a number of different functions. These have somehow or other to be correlated within the plant, in order to produce the observed effect. Nutrition obviously plays a part, though how large or important it is we do not know; but at least it is essential, if only as providing the means for thickening the cell walls. It is, however, very clear that the causes underlying the adaptive character of the *distribution* of the tissues are still far to seek, and much more detailed analysis of the life processes are required before we shall be able to trace, even in outline, the actual relations of cause and effect. We have as yet no certain or definite knowledge of the physical machinery of heredity. We do not know why one plant reacts in this, another in that manner towards an apparently identical set of external conditions. But we have reasons for believing that the difference lies somehow and somewhere in the obscurities of individual or racial character which in turn are dependent on differences in physical and chemical constitution. But as yet we can do little more than guess wherein the nature of these differences may lie.

# CHAPTER XII

## RELATION OF PLANTS TO WATER

We have already become acquainted with the manner in which the ordinary land plants absorb the water they require. Now water plays so significant a part in connection with all the principal functions of living things that a closer examination of the matter will reveal much that is of intense interest, and of great importance in its theoretical bearings on the problems already adumbrated.

The urgent need of water, common to all vegetation, is especially great on the part of the green plants, although the larger portion of that which is absorbed is not used directly in the synthetic functions, but is exhaled through the stomata with which most leaves are so plentifully provided. Its value to the plant stands even before that of light, for photosynthesis, like other characteristically vital functions, is practically arrested as soon as the supply of water falls below a critical amount.

Some of the higher and many of the lower green plants are able to tolerate long periods of drought; but they do so by passing into a condition of suspended animation, during which many of their chemical processes are slowed down and others are completely arrested. Thus a large number of lichens, certain mosses, and various other plants, may all become so far desiccated during dry periods that they can be easily reduced to powder. A shower of rain, however, serves to restore them in a few minutes to a condition of renewed and active vitality.

Nearly all land plants are liable to encounter periods during which the supply of available moisture runs short. The shortage may be due to seasonal or climatic causes, or it may be incidental to the particular kind of habitat in which a plant is growing. For example, plants which live on bare rocks, or on tree trunks, are evidently exposed in a greater degree to intermittence in water supply than those which are rooted in the soil. We find that such *lithophytic* and *epiphytic* vegetation is especially rich in species that exhibit wonderful adaptations to their own particular environment, adaptations which enable them successfully to cope with the difficulties and disadvantages that so obviously face them.

A somewhat wider survey of the water problem as it affects vegetation generally, shows that it is necessary to distinguish clearly between that kind of drought which is merely *physical*, i. e. is due to actual scarcity of water, and another kind which may be more properly described as *physiological.* In the latter case a plant, however favourably it may seem to be situated so far as access to water is concerned, may nevertheless be unable to absorb it in sufficient quantity.

This may happen when the temperature of the medium is too low; for the active absorption by roots is only possible within a rather narrow range of temperature, the limits varying somewhat for different plants. Or the water itself may contain substances in solution which prejudicially affect the exercise of the absorptive functions. Thus the water of salt marshes, as well as that which saturates the soil of peaty moorlands, is not available for the vast majority of plants, and they are consequently precluded from occupying regions where such conditions prevail. Those plants which do tolerate or even demand them, often take in relatively small quantities of the water, and they have in consequence to limit the amount lost as vapour in transpiration. In connection with this limitation a variety of subsidiary modifications of habit may become manifest. Slowness of growth, succulence, or the opposite character of spininess, are common features; whilst an evergreen habit with leathery leaves is of fairly frequent occurrence amongst the perennial plants of such localities. Indeed, experience shows that any circumstance tending to reduce the amount of available water, whether due to physical or physiological conditions, will stamp its impress on the vegetation.

The onset of a period of drought will speedily result in the extinction of entire species within the affected area, and their places will rapidly be taken by others which are already adapted to these new conditions. Which of the many possible forms of adaptedness to drought a particular colonist may possess, depends of course on its own inherent and hereditary properties. The part played by the environment in the matter is merely to rule out all those plants which are not previously fitted in one way or another to conform to its requirements, and to tolerate the limitation which it imposes.

It is necessary, however, to observe the greatest caution in concluding, as is sometimes done, that the various "adaptations" to dry conditions are to be attributed offhand to a faculty assumed to be possessed by the plant which enables it to make a direct and appropriate response to the demands of the environment in question. As a matter of fact many plants are incapable of making any purposive response at all; and the matter is by no means a simple one even in the case of those which can so react. The constitution of the living protoplasm is the main factor which determines the nature of response to water requirements, no less than to mechanical needs. It is only those plants, the living substance of which has become definitely altered in certain (but alternative) ways, that are capable of exhibiting adaptations (or adaptedness) towards a particular set of external conditions. The successful reaction is commonly bound up with complex internal functional relations, and among these nutrition often plays a leading share. It may happen, as in the formation of winter bud scales (see p. 142), that the functional conditions which are more immediately concerned in the formation of "adaptive" structures ensure their production quite independently of their ultimate utility as protective organs during the winter months.

The behaviour of plants at the different seasons of the year is instructive from this point of view.

The habit of shedding the leaves on the approach of winter which is so characteristic of the majority of our trees and shrubs is often regarded as an adaptation to physiological drought rather than as directly due to the action of the lowering of temperature on leaves. Although there is plenty of water in the soil in winter, the temperature of the ground is too low to enable the trees to absorb it freely enough. It is true there are evergreen trees which do not throw off their leaves in autumn, but they generally exhibit definite structural features indicative of a normally slow rate of transpiration, *i. e.* of water lost as vapour through the stomata. The leaves are leathery or small, the stomata are comparatively few, whilst various other features point to an economy in the matter of water expenditure. The deciduous trees and shrubs, which shed their leaves in winter, are relatively more prodigal of water during the warmer season, thus compensating for the alternate periods of inactivity.

Without doubt there is much to be urged in favour of the deciduous habit being regarded primarily as an adaptation to a reduction of the water supply. This argument is strengthened by a consideration of plants which quite definitely respond to periodic drought, physical or physiological, by casting off their leaves. Thus, in the tropics the dry season is marked by the leafless character of many trees which renew their foliage as soon as the rainy season sets in. Again, many evergreens, when transplanted, frequently throw off their leaves. This is the result of injury to, and disturbance of, the root system, whereby absorption is suddenly checked. Hollies and laurels often display this reaction, and indeed it is generally to be regarded as a favourable sign for the future of the plant; individuals that shed their leaves promptly always suffer less than those which retain their foliage in a flaccid or withered condition on the branches.

But if we look a little further into this question of leaf fall, it turns out to be not so simple as it appears at first sight. It must be premised that the fall of the leaf is not a matter of mere detachment, but it ensues in consequence of definite changes which have caused a layer of tissue to become differentiated across the base (usually) of the leaf. Thus, even before the detachment of the leaf, the wound is practically healed in advance. Although various functions connected with nutrition are concerned in bringing about the formation of this "separation layer," the most powerful stimulus is unquestionably that of physiological water starvation, whether this starvation results from physical shortage or from a physiological inability to absorb. The intermittent periods of drought in summer are often followed by early leaf fall on the part of the more intolerant trees such as the lime. The evergreens, on the other hand, are usually very long suffering, but, as we have seen, a severe diminution of water supply is, or may be, followed by the hurrying up of those internal processes which culminate in the differentiation of the separation layer at the base of the leaves.

Thus a plant which is fitted for average conditions of water supply (and is often therefore called a Mesophyte) may assume certain of the distinctive characters of plants fitted for dry conditions, when its supplies of water are from any cause suddenly interfered with. Plants which are specially adapted to dry conditions are called Xerophytes, and they are directly contrasted with the Hygrophytes, *i. e.* with those restricted to very wet surroundings.

In the examples we have just considered, the adaptedness to dry or xerophytic conditions is attained by reduction of the transpiring surface. This is a very common feature of xerophytes,[1] and it forcibly illustrates the limitation of one important function (that of

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[1] Not *all* plants with reduced leaf surface are xerophytes. The large Water Rush (*Scirpus lacustris*) used in the manufacture of rush-bottomed chairs is an instance. The reduction of the leaves, and the transference of the photosynthetic function to the stems of these plants is certainly to be correlated with mechanical requirements. A plant built on the plan of the water rush would be an impossibility if any weight of green foliage had to be sustained.

photosynthesis) by another factor which also influences the process of nutrition as a whole.

The reduction of leaf surface, which is of intermittent or annual occurrence in our everyday vegetation, may become the normal state of a more specialised xerophyte. The leaves may be very small, or they may even be practically absent so far as photosynthetic function is concerned. In such plants, however, this office may continue to be discharged by the stems, which remain green, and thus to some extent may take the place of the leaves. Their special advantage in this connection is mainly due to their structure, and to the relatively small number of stomata, which enables them to check the escape of water from the plant.

It is a singular fact that when a species or race has once exhibited a tendency towards the loss or atrophy of an organ, *e. g.* the leaf, the descendants commonly appear to be unable to check it. If any of them vary in such a way as to increase their green surface, this is effected not by enlarging their diminished leaves, but by flattening and specialising some other organ. Sometimes the process may even be seen to accompany the diminution of the leaves, as in some species of acacia. In *Acacia melanoxylon*, for example, we find the leaf stalk gradually flattening, and assuming the functions generally undertaken by the blade, which becomes completely atrophied. Other species of acacia show the same tendency in a still more advanced degree. Only a few of the earliest leaves on the seedling exhibit a blade, all the succeeding ones having flattened petioles only.

More often, however, it is the stem which undergoes modification and develops leaf-like characters. When only certain branches become specialised in this way, as in species of Butcher's Broom (Ruscus), it may require careful examination to detect the cauline nature of the apparent leaves. But the genuine leaves are really present, and although they are reduced to small brown scales, they suffice to indicate the true condition in this as in other extreme examples.

A still more remarkable modification is seen when the *roots* assume the functions of green leaves. An instance of this is furnished by the genus of epiphytic orchids known as Taeniophyllum (Fig. 18). These orchids, which possess very inconspicuous flowers, are also destitute of foliage leaves. But the function of photosynthesis is discharged by the green, band- or tape-like roots which are appressed to the bark of the trees upon which the plants are growing. In some species the roots are very long, and hang freely from the tree trunk, when their resemblance to narrow strap-shaped leaves becomes additionally striking.

It often happens that new structural modifications—adaptations in the making, as it were—respond to the influence of the stimulus of light in a remarkably purposive fashion. Thus nearly all the cacti, in their adult stages,

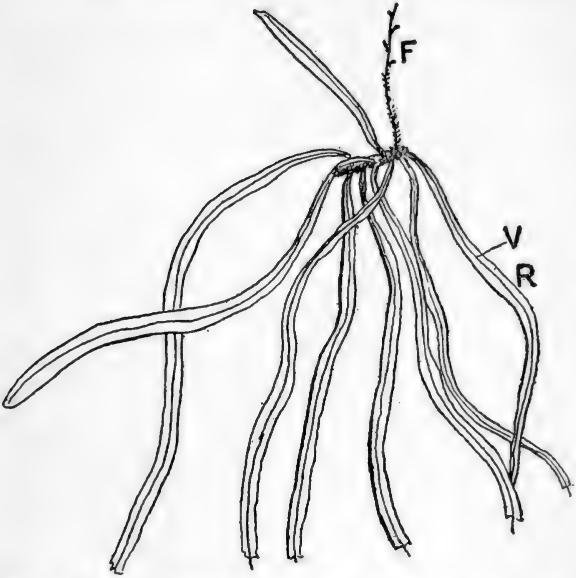

Fig. 18.—*Taeniophyllum torricellense,* an orchid with green, flattened, leaf-like roots. R, roots; V, vascular strand; F, flowering spike. (The roots are shown broken off at the ends; they are actually much longer than indicated in the diagram, which was made from a specimen in the Natural History Museum, S. Kensington.)

are destitute of green leaves, their stems functioning as the photosynthetic organs. Some of them, like the species of Phyllocactus, often grown for the sake of their beautiful flowers, bear a strong resemblance to lobed, fleshy leaves. They are, however, merely stems, flattened by the action of light, which is probably indirectly operative through nutritive processes. If the phyllocacti are grown in the dark they only produce rod-like stems, very different from the leaf-like shape assumed under ordinary conditions of illumination.

The cacti furnish a remarkable range of forms. All of them are pronounced xerophytes. Now it is a curious fact that these plants of the Western hemisphere have their doubles in some of the euphorbias, or spurges, of the hot, dry regions of the Eastern tropics. So faithfully, indeed, are many of the leading types of cactus forms reproduced, that an untrained observer may easily be deceived. No satisfactory explanation has been given for the occurrence of these closely similar forms of plants, which are widely sundered in affinity and properties, as well as in their geographical distribution.

The ordinary winter buds of our trees and shrubs, with their protective scales, provide us with still other adaptations by which loss of water from the enclosed leaves is prevented. The young leaves, since they are not only very thin, but are imperfectly protected by a cuticular surface, would assuredly suffer if they were exposed to the air. This is probably the chief function of the bud scales, though doubtless they further serve to protect the delicate leaves within from a variety of other injurious influences. Nevertheless, in spite of their wonderfully perfect adaptation to these functions, they may be shown to owe their existence in their present form to certain conditions which affect nutrition during a far earlier period of active vegetation, for they are simply modified leaves or parts of leaves. In a sense they may be said to have been starved and arrested, or rather distorted, in their development. This can easily be proved in such a plant as a young ash or a plum, by pulling off the young and active outer foliage leaves. The operation must be performed quite early in the summer while the bud scales are young, and before they are fully formed. The result of the experiment is to cause the young leaves that otherwise would have been destined to form the bud scales, to grow out, and provide a further crop of foliage leaves. The removal of the active leaves has diverted nutrition into the young bud scales that were to be, and has caused them to assume the form and character of foliage leaves; and this happens for precisely the same material reasons that the foliage leaves themselves are forced to assume their own proper form.

In many parts of the world the climate is sharply marked into a wet and a dry season. During the wet period, vegetation of a mesophytic type can exist; but unless it has some special adaptation to tide it over the dry, and often hot, time of year it would be unable to occupy such climatal regions. Often the adaptation is fairly obvious. Thus, when the rain falls on the South African veldt, innumerable leaves and flowers spring up as if by magic. They flower and fruit, and then disappear for the rest of the year. A relatively large proportion of this vegetation consists of perennial plants of a bulbous or tuberous character. As long as the dry weather lasts they remain in a resting condition, the bulbs or tubers showing no sign of life. If they be cut open, they are found, even at this season, to be juicy; that is to say, they store water and retain it with great tenacity. When conditions become favourable, the leaves rapidly develop, and they are often not at all the leathery or even succulent structures one might expect to meet with. In fact they frequently resemble those of typically mesophytic vegetation, and are thus simply adapted for an average water supply, and indeed such conditions do actually prevail during their period of active growth. Their food manufacture goes on rapidly, and the surplus is stored up in the swollen portion, so that when the growing, moist season is over, they will have accumulated an amount of easily utilisable food. It is the possession of these qualities which enables them to form underground the flowers and leaves which will expand so rapidly on the return of the rains. Everything is almost complete, and is ready to push above the ground at a few days', or even a few hours', notice.

This form of response to periods of drought, namely the capacity to store up food, and even water, is very widespread, but one must not imagine that *all* bulbous plants are to be looked on as xerophytes, though the bulbous habit undoubtedly does confer on its possessor the power or faculty of colonising localities such as those just indicated. Many of our spring woodland plants are bulbous or tuberous; but in their case it is not so much a question of drought as one of light.

The bulbous character of the wild hyacinth, for example, enables it to thrive in shady woods, even under beech and hornbeam, for, like its relatives in the open field, it is provided with a large stock of available food in the bulb scales, which was manufactured and stored up during the preceding spring. When the warm weather returns after the winter the hyacinths rapidly sprout, and their green leaves are fully exposed to the light. Later on, however, as the trees unfold their leaves the light soon weakens, and little or no photosynthesis can go on under the dense shade of a beech wood. But by this time the plants have done their work, and have already laid up a stock of food for the following year. Their leaves die down, and only the ripening seed capsules reveal their presence in the wood.

The hyacinth is by no means necessarily a woodland plant. In many parts of Wales and Scotland it grows amongst the grass in the open fields, wherever it is able to compete with the growing herbage.

The point which the hyacinth enables us to emphasise is this, that whilst the bulbous (or tuberous) habit is one which will put its owner into favourable relation with certain types of dry climates, it will also, and for analogous reasons, prove an adaptation suitable for other and very different conditions as well, provided that these also include a brief period favourable to the vegetative activity of the plants.

When the climate is persistently dry the vegetation is usually mixed and consists of plants which are either succulent or spiny. These seem contradictory features, and in a measure so they are. Nevertheless, each habit, that of succulence and that of spininess, is well adapted for dry climatic conditions. The succulent plant stores what water it can get and when it can get it. A remarkably extensive and deep root system is often developed, by which it is enabled to search the ground thoroughly and effectively for the requisite moisture. Moreover, such water as it does acquire is lost very slowly, owing to peculiar features connected with the stomata. The presence of wax or " bloom " also serves as an additional check to the escape of watery vapour.

The spiny plants are similarly built on lines calculated to limit the output of water, though why the reduced branches and leaves should so commonly assume the form of spines it is not easy to say. The supposed function of the spines in keeping off browsing animals is a ready, but not very satisfying, explanation.

Observation teaches that both classes of plants, the spiny and succulent, are of comparatively slow growth. But it is not quite correct to assert of xerophytes generally that in their habits and rate of growth they compare unfavourably with the mesophytes. The truth rather is that they are able if need be to support life on a very limited income, by cutting down their expenditure in various directions. It is by this faculty of exercising economy that they are enabled to flourish in regions from which the less hardy mesophytes are excluded. A large number of xerophytes are, however, by no means solely adapted to a life of austerity. Transplanted and grown under ameliorated conditions, they often respond to the change by a rapid and vigorous growth. It seldom happens, however, that they are able to hold their own in competition with the mesophytes in a natural environment suitable for the latter, and they commonly become killed out sooner or later by their more vigorous rivals.

There are a few of the highly specialised xerophytes, such as cacti, which are so definitely modified in relation to conditions of drought that they have become extremely intolerant of moisture, even in quantities such as would barely suffice to keep an ordinary mesophyte alive. Plants such as these stand at one extreme end of the scale of vegetation, the other end being occupied by the genuine aquatics or hydrophytes which also are unable to endure mesophytic conditions, because they lose water too readily. Different as are these extreme examples from one another, they yet agree in this respect, namely that the chemical processes characteristic of their vital functions are incapable of becoming so modified as to produce the kind of structure suited to average mesophytic conditions. In the case of aquatics the general nature of this defect is clearer than in the xerophytes, and mainly depends on the inability to form a suitable cuticle, added to which the functions of water conduction and mechanical support are often inadequate for a terrestrial habitat.

# CHAPTER XIII

## THE EPIPHYTES

HITHERTO we have chiefly considered the relation of vegetation to an exiguous water supply rather from the point of view of parsimony. A short or precarious supply is met by reducing the output, hoarding the precious liquid, or living an abstemious life.

But other plants have shown greater powers of invention, so to speak, in overcoming the difficulties of life. They have countered intermittence by the construction of more or less ample cisterns, and they have developed new methods by which the available water is absorbed. These modifications of structure have rendered existence possible, and even easy, in many situations from which ordinary plants are debarred from establishing themselves. Perhaps the best examples of this inventive resourcefulness are to be met with amongst the plants that have exchanged a terrestrial for an arboreal habitat. Such plants are generally called epiphytes. They are in no sense necessarily *parasitic*, that is to say they do not tax their host for food. All they demand from the trees is the space whereon to grow.

The epiphytes form a large class, and they include many of the humbler members of the vegetable kingdom as well as a considerable number drawn from the highest ranks of flowering plants.

They exhibit all grades of adaptedness for the acquisition and storage of water. At the lowest end we find some of the simpler forms, especially amongst the algæ and mosses, which will stand complete dessication. But there are other species of mosses, and especially of the nearly related family of liverworts, which have advanced far beyond the attitude of mere tolerance, and not only exhibit adaptation for rapid water absorption, but also possess means of storing it during a time of plenty. In some liverworts tuberous bodies are formed, and during the dry season these alone persist, to break out into growth as soon as the rains commence. In the leafy forms it often happens that some or all of the leaves are modified so as to form bottle-like receptacles (Frullania, Physiotium, etc.) for water.

It is amongst the ferns and flowering plants, however, that we find the greatest diversity, and perhaps we might add perfection, in the adaptations to solve the problems connected with a precarious and intermittent water supply.

It is true that the majority of the highly specialised epiphytes are more or less restricted to regions of large and fairly frequent rainfall, but others are able, owing to certain peculiarities of structure and habit, to endure recurrent periods of drought provided that they do not suffer too much in this respect during their season of active vegetative growth.

Disregarding, then, the less highly specialised epiphytes, which respond to a dry season by simply closing down their vital processes, we will turn our attention to the more highly adapted types amongst the flowering plants.

The orchids will serve as our first examples. A large proportion of the members of this family are not epiphytic at all, but grow in the ground. Even there they exhibit many deviations from the typical structure of roots, but in a number of the epiphytic species, so common in the tropical forests, the root-system undergoes a remarkable and adaptive change of structure. Whilst some of the roots may depart but slightly from the form commonly met with in these organs, and serve to fasten the plant to its arboreal perch, others are thicker, often green, and when dry are of a white or lustrous grey colour. The whiteness is due to the presence of air in the outer layers of cells which form a very peculiar sheathing mantle on the root. In ordinary roots there is but one well-defined layer sheathing the rind and giving rise to the root-hairs; but in these orchids it divides and forms many layers, whilst the root-hairs are usually suppressed. The illustration will better explain what is meant, and will serve to bring out the more salient features of this remarkable structure, which is generally known as the *velamen* of the orchid root (Fig. 19).

The cell walls of the velamen are strengthened by bars of thickening, which gives them a spiral or netted appearance under the microscope. The function of the velamen as a whole is to act as a sort of sponge which soaks up liquid falling on it with extreme rapidity. Thus the plant is able quickly to replenish its supplies of water during a shower. In many orchids the bases of the stems and sometimes the leafy joints are swollen with the so-called "pseudobulbs," which form additional storehouses for the water thus obtained. During the periods which intervene between the rains, the plant often throws off its leaves, its flowers drawing on the water supplies stored in the pseudobulb. The surface of the latter becomes more and more wrinkled as its storage cells become depleted of their water contents.

The roots, although specialised in the way described above, have retained, in many instances at any rate, the power of growing like ordinary ones if they should happen to penetrate the substratum. This sometimes occurs when there is sufficient vegetable detritus caught in the orchid clump, or when the root penetrates a piece of damp rotten wood. Root-hairs are then produced, and the velamen may be scarcely produced at all.

It is a remarkable fact that some of the

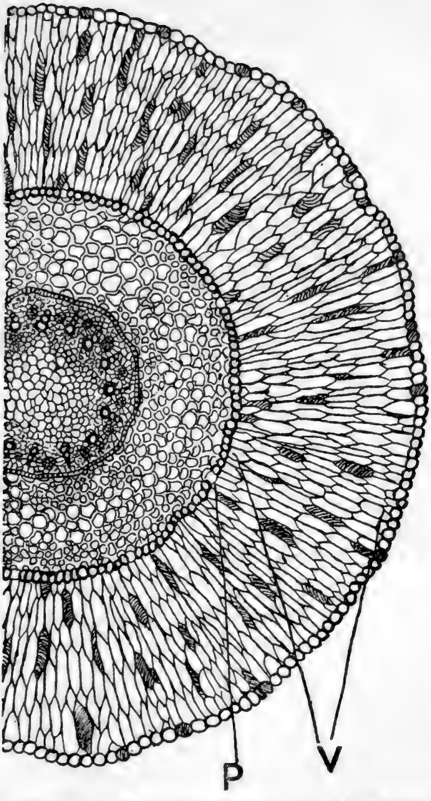

Fig. 19.—Transverse section of an orchid (*Dendrobium*) root showing the velamen (V). Note the thin-walled "passage-cells" (P), through which the water gains access to the interior of the root.

epiphytic members of a very different family, the aroids, have also, and independently, acquired the faculty of developing a velamen which is closely similar to that formed by the orchids.

It is very easy to see that the presence of velamen is of great use to a plant growing as an epiphyte, but that is not at all the same thing as accounting for its presence. It certainly enables the plant to take advantage of such positions as the trunks of trees, where it becomes lifted up to the light, and enjoys various other advantages. But how has it come about that it is just developed in these orchids (and aroids) in response to their particular needs, whilst the innumerable epiphytes belonging to other families of plants have not altered their roots in this striking manner ? We cannot tell—at any rate at present.

The same difficulty in giving a real explanation is inherent in every problem of plant (and animal) form, but it is often slurred over, especially when the structure is obviously of use in a particular connection. To describe it as an adaptation to a particular condition of the environment is merely to state an impression. Such descriptive phrases furnish no explanation of origin, nor do they illuminate in any material degree the hidden relations of cause and effect.

There are other flowering epiphytes which absorb water not by their roots at all, but by curiously developed hairs on their leaves. Examples of this habit are afforded by the Tillandsias, and other Bromeliads of the tropical forests of the Western world. The roots may be altogether lacking in some species, and even when they are produced they merely serve to attach the plant to a branch, and function only slightly, or not at all, as water-absorbing organs. *Tillandsia usneoides*, common in the damp West Indian forests, possesses no roots; it bears sickle-shaped leaves which readily become entangled in small twigs, and the greyish-green festoons of this plant, as they hang down from the branches, resemble luxuriant lichens rather than a flowering plant. Indeed, the resemblance is so great as readily to deceive any but a careful observer.

The epiphytic tillandsias absorb the whole of their water supply through remarkable hairs which clothe the surfaces of the plant. The accompanying figure illustrates their general appearance and structure (Fig. 20). From a slight depression there arises a stalked hair, the upper portion of which is flattened out as a membranous expansion consisting of many cells arranged around the central group that terminates the stalk. The cell walls on the upper surface of the hair are very thick, but they are practically destitute of a cuticle, and water probably can pass through them as well as through the walls on the under surface which are much thinner.

The flattened membranous tops of the hairs often overlap. and when water is dashed on

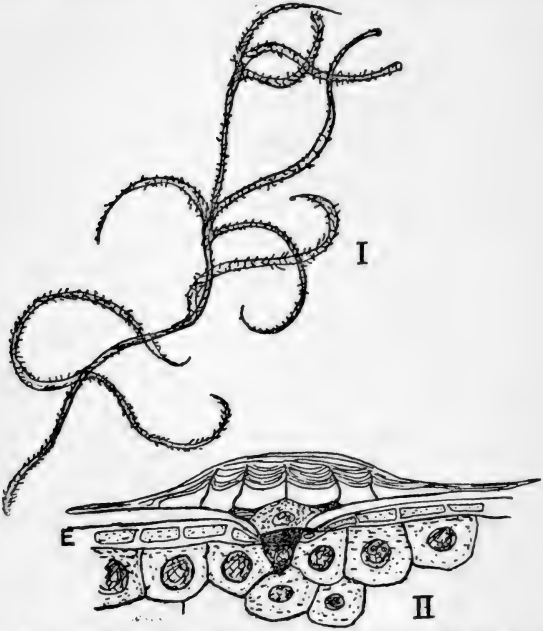

Fig. 20.—*Tillandsia usneoides.* I.—A portion of the leafy stem, showing the curved form of the stem and leaves. II.—One of the hairs on the leaf in section (highly magnified). The water which is soaked up by the hair passes by the darkly shaded cells into the interior of the leaf. E, epidermis of the leaf.

the plant it is held amongst them by capillary attraction, the displacement of the air by water causing the grey colour to turn green. Water rapidly passes into the cells of the hair and thence is transmitted to the leaf. As the air becomes dry again the hair gradually flattens down, and its thick outer wall serves as an additional barrier to prevent undue loss of water from the leaf.

It is obvious that tillandsias, and other plants which, like them, grow on the branches of trees, must be largely dependent on somewhat casual sources for the small supply of mineral salts which are required for their subsistence. Most of it reaches them in the form of dust, or as vegetable detritus of various kinds. Inasmuch as the leaf-hair, like the root-hair, can only absorb substances already in solution, it becomes a question of some interest to ascertain whether the salts really do pass into the plant in this way, and if so whether the absorbent hairs of the epiphytic tillandsias differ in this respect from their near relatives which still grow in the ground.

It has been ascertained that salts *are* so taken in by the epiphytic species, but, as might be expected, not necessarily or commonly so by the rest. The Pine-apple, a terrestrial plant related to Tillandsia, possesses hairs similar to those of the latter plants, on its leaves. They are able to absorb water, but the salts dissolved in it do not pass in, for they cannot traverse the protoplasmic lining of the cells.

Many of the other members of the natural order (Bromeliaceæ) to which the pine-apple and the tillandsias belong, are variously specialised with respect to water supplies. The large bromeliad of tropical America possess clasping roots which fasten the short stem with its, relatively speaking, immense crown of foliage, on the branch of the tree which serves as its perch. The roots have little if anything to do with absorption, a function which has been almost entirely taken over by the tillandsia-like hairs which are found on the upper surfaces of the leaves. The latter form remarkable cisterns in which water is collected and stored, and from which it is absorbed by the hairs that are especially numerous where the water is stored. Each leaf is a long, more or less strap-shaped body, with the edges curving towards each other in the middle portion, thus forming a sort of gutter. Nearer the base, the leaves press tightly on each other and thus constitute the cisterns. Water falling on the upper surface of the leaf is directed into them by means of the gutter-like curvature just described, which causes the rain to run down to the centre of the crown, instead of dripping off as it does from most leaves. The efficient manner in which the foliage is arranged to form cisterns may be gauged by the fact that water plants are fairly often found growing and flourishing in the water thus collected and retained.

Another plant, *Dischidia rafflesiana*, belonging to the very different family of Asclepiads, may be considered in this connection though it is not strictly speaking an epiphyte. It commonly grows on rocky surfaces, but it is subjected, like the epiphyte, to the need of special adaptations for obtaining water. Its ordinary leaves are rather thick and fleshy, and thus are to be regarded as dealing economically with such water as may be available. But some of its leaves undergo a most remarkable modification in the course of their development, and assume the form of pitchers. The mouth of the pitcher is directed upwards, and they are readily filled by the heavy showers that prevail in the regions of the Eastern Archipelago and Malay where the plant occurs. The utilisation of the water is finally effected by small branching roots, which spring from the stem close to the insertion of the leaf pitcher. These enter it and ramify inside it. Often detritus of various sorts becomes washed into the pitcher, and thus it not only serves to collect water, but it actually provides soil for the plant as well.

A few of the epiphytes have been chosen for consideration here because they so admirably illustrate the remarkable methods by which the difficulties of obtaining water have been overcome. An extended study of these remarkable plants would have shown this more in detail, for there is hardly any conceivable device which has not been actually put into practice by one or another of them. But whatever be the particular nature of the adaption in any given instance, its final significance, and its ultimate justification, is to be sought in the assistance it renders towards the proper discharge of the photosynthetic functions of the green surface.

Plants which contain no chlorophyll—and there are vast numbers of them—have no use for the varied complications that circumstances may render essential or ancillary to the green members of the vegetable kingdom. Indeed, it is not too much to say that all the beauty of form, all the elaborate structure, which is so copiously displayed by the vegetative organs of trees and plants generally, spring from the possession of this substance chlorophyll, with its wonderful power of trapping and utilising the energy of the sunlight.

But apart from all æsthetic considerations, and regarding the matter solely from the most material point of view, we may further assert that the elaboration of chlorophyll has been fraught with consequences to the whole organic world compared with which all the other structural products of evolutionary change sink into insignificance and obscurity.

# CHAPTER XIV

## THE FUNGI

We may now turn our attention to a very different type of vegetation, the members of which are wholly, or almost wholly, lacking in chlorophyll. The fungi and bacteria are typical representatives of these non-green organisms, but a certain number of the higher flowering plants have also departed from the way of their ancestors, and have lost their green colour. It is a significant fact, which strikes us at the very outset, that every one of these colourless flowering plants live on ready-formed organic matter derived either from dead or still living organisms.

As a class, the plants which lack chlorophyll are distinguished by the relatively simple structure of their vegetative organs, although their reproductive organs may, on the other hand, be very complex. For example, the somewhat elaborate objects popularly known as " fungi " are not the vegetative bodies of the fungi at all, but only their fructifications. Flowering plants which have adopted the non-chlorophyll habit similarly tend to become greatly modified in everything except their reproductive organs—the flowers and fruit. We often speak of them as degraded or degenerate forms, but this is a somewhat loose and inaccurate form of expression. The vegetative structure has, it is true, been *simplified*, but in such a way as to render the plants much better adapted to the new conditions of nutrition than they ever could have been had they retained the complexity appropriate to the green ancestral type.

For the moment we will pass over the bacteria, which differ in many respects from other plants, and survey the most salient features presented by the fungi.

Fungi, like the flowering parasites above mentioned, have descended from green ancestors, but it is among the lower ranks of the vegetable kingdom that their origin is to be sought. It is tolerably certain that the class of fungi, as we know them to-day, represent a number of not very closely related families, and that these have descended from more than one chlorophyllous algal stock. There is no reason, therefore, to think that their vegetative structure has undergone very important alteration in the direction of simplicity. It would probably be more in accordance with facts to say that it has never emerged from a primitively simple type of organisation.

The body of a young, actively growing fungus consists entirely of simple tubular threads, or *hyphæ*, which, in the majority of species, are partitioned by cross walls. These hyphæ ramify over and through the nutrient substratum, and sometimes they cohere in strands. They then become easily visible to the naked eye and are popularly known as "spawn." The spawn thus represents a specially luxuriant condition of the vegetative body or *mycelium* of the fungus, the mycelium being taken as a collective term for the mass of hyphal threads of which the vegetative part of the fungus is composed. Even the "toadstools" and other fructifications of fungi are entirely produced by the organised weaving of the hyphæ into more or less solid structures, followed by differentiation in the mass thus formed, together with the specialised growth of certain groups of hyphæ.

The fungus obtains the whole of its food from the substratum in which it is growing, and some of the nutriment is always of organic origin. Inasmuch as the fungus contains neither chlorophyll, nor any other material which would enable it to utilise the energy of sunlight, there is no necessity for the growing mass to expose itself to light at all. Indeed, to do so would carry with it the manifest disadvantages of removing it from the immediate source of nutrition, as well as of exposing it to the risk of desiccation.

Now, having regard to the fact that the vegetative plant of the fungus is absorbing the whole of its food in a dissolved form from the material in which it is ramifying, it will be evident that the larger the surface, in proportion to the bulk of the fungus, the better this process of absorption will go on. Consequently, we can easily understand that, up to a certain point, the simpler the structure, and the more independent the individual mycelial hyphæ are of one another, the more thoroughly the plant is adapted to explore its nutrient surroundings and to absorb its food. As with the root-hairs of a root, increase of surface is the keynote of the performance. We find that all non-green plants tend towards this adapted simplicity of organisation, though the higher green plants have far to go before they can shake off the shackles of complexity. It is only from an anthropomorphic standpoint, then, that we can regard these plants as merely degraded or degenerate, for they are just as accurately adapted to obtain their more specialised form of food as is the complex green plant in relation to its simpler sources of nutrition.

Furthermore, from this physiological point of view, the fungi are even more complex than their green ancestors, for they do not merely absorb, but they also profoundly influence the nature of the substratum in which they live by means of the ferments and other substances which they excrete. Some of these non-green plants show an almost diabolical ingenuity of physiological action, as, for example, when some of the parasites, by emitting an attractive excretion, cause their victims to actually grow towards them.

Although the fungi, as a class, are dependent for their nourishment on substances which have originated from other living things, they differ a good deal among themselves as to the kind of food material they can use. Some are dependent on the living bodies of animals or plants, and then we call them *parasites*. Others live on dead or decaying remains, and are commonly termed *saprophytes*. The saprophytes are a very extensive class, and include many species that can live on relatively simple organic residues such as sugar, organic acids, and so forth. But these simpler feeders are connected with more obviously saprophytic types by all conceivable intermediate forms, and even the distinction between saprophytes and parasites is far from absolute, for many saprophytes can become parasites, and *vice versa*.

Now the utilisation of all food, regarded as a means to an end, is connected with changes in the states of energy. Complex organic substances possess a considerable amount of energy in a locked-up, or *potential* form, When the food substances undergo oxidation and are broken down into simpler ones, the potential energy is set free as *kinetic* energy, just as happens when a piece of coal is oxidised or burnt. This kinetic energy is directly available for doing work, and may be utilised to boil a kettle or to build up the body of a fungus. In the former case, the kinetic energy is used to alter the physical state of the water; in the latter, it is used to construct complex out of relatively simple chemical substances. And in this process the energy, instead of becoming dissipated over an infinite field, is concentrated within narrow limits. It is again locked up as potential energy in the construction of chemical molecules, and it can be reconverted into the kinetic form when the molecular groupings once more break down.

We have already seen that the various organic substances on which the fungi and other colourless parasites and saprophytes subsist are all traceable more or less directly to the synthetic processes of the green plants. The latter are empowered to build up this organic material by utilising the energy of the sunlight for the work. Thus we are justified in saying that the products of photosynthesis practically represent the total means available for supplying the energy required to drive the machinery of the rest of the life of the world. In other words, the potential energy of the organic food is resolved into kinetic energy in the body of an organism, and it is solely by virtue of this kinetic energy that an organisn can live and move and have its being.

Now the essential chemical process which is carried on when the energy of the sunlight drives the photosynthetic machinery of the green plants results in reduction or deoxidation. The carbohydrate food—the tangible result of this process—represents a store of energy equal to that required to tear the oxygen away from the various parts while it was in the making. This energy can be again released in the kinetic form by oxidation. But it need not take place in one stage. We shall get a certain definite amount of kinetic energy set free if we burn a pound of sugar, but we can break up the sugar more gradually, and at each stage a definite amount of energy will be liberated. It is only when we have completed the destructive process, and carbon dioxide and water alone remain, that we can get no more energy from our sugar products. And if we were to add up the various amounts of energy liberated during the various stages of destruction of the sugar, they would amount to the same figure as if we had burnt (*i. e.* oxidised) it at once.

Of course, neither an animal nor plant can ever burn itself completely down to the simple substances into which it is capable of being resolved. Some portions of it will remain intact, and of the rest all sorts of intermediate products will be formed. These possess different energy values according to their composition, and especially according to their complete or incomplete state of oxidation.

It is on these intact or partially broken up chemical substances that the non-green organisms are able to live, and the fungi and bacteria especially serve an important purpose in the world because they are able to induce the breaking up of the complex substances constituting the dead bodies of other organisms into simpler chemical compounds, and sometimes even into their elements. They utilise a certain amount of the energy thus finally set free in building up the materials of which their own bodies are constructed, but the proportion of matter (and of energy too) thus locked up again is extremely small when compared with that which has been liberated in the process.

Regarded from this standpoint the sun is seen to be the very fountain of life and power. The complex materials which jostle each other as they are borne down the stream of life break down here, provide the power for synthesis there, but on the whole are ever losing more of their energy, for some is continually dissipated as heat. Many of the useless molecular fragments which drift out of the stream of life are presently caught up again at the fountain-head, the chlorophyll machinery driven by the solar energy once more draws them into the mill, there they are broken up, are compounded with other ingredients, and the whole turned out once more as energy-containing carbohydrate. Again the compounded matter re-enters the stream of life, to part, little by little, with the energy it contains. Some is destined to reappear in vital units of almost infinite complexity, the rest is utilised or lost in various ways, and the broken and buffeted fragments of the carbohydrate are once more cast forth into the inorganic world as simple and vitally useless molecules.

Let us take a specific instance by way of illustration of the foregoing consideration. Wood is an almost imperishable substance, at least under ordinary circumstances, and so long as it is preserved from the attacks of living organisms. But timber is liable to the depredations of a large number of different fungi which, under conditions favourable to their existence, are able to use it as food. They act on it by various ferments, bringing some of its constituents into solution, absorbing and partially breaking them down. The wood is soon reduced to a friable mass, weighing far less than the original timber, owing to the decomposition of its chemical substance, and the elimination of some of the products of its oxidation. Even the solid residue will soon disappear under the further influence of a succession of micro-organisms, which will finally disintegrate whatever the fungus may have left. Thus, in course of time, the whole of the chemical materials out of which the timber was constructed will again become part of the floating capital of nature, available for the constructive processes of new organisms, or destined for yet other purposes in the chemical change going on in the world.

Most timbers are liable to infection by fungi when they are stored in a damp condition. The danger is greatly accentuated if the wood contains organic matter which is either soluble or easily rendered so, and this is one of the reasons why trees are felled at a time of the year in which the wood naturally contains least moisture or sap, and why the tree is, or should be, left to "season" (*i. e.* to dry) before being cut up. A source of danger to stored timber may arise from contamination with organic matter consequent on the neglect of proper sanitary precautions. For wood which is so contaminated forms a very suitable substratum for the germination of a number of pests, and attacks of the dangerous "dry rot" fungus (Merulius) has sometimes been traced to this source. When once a wood-destroying mycelium has established itself in a piece of timber it may be difficult to get rid of it. It will often lie dormant for a considerable time when the wood is dry, and only moisture or dampness is required to awaken it to dangerously active growth.

The wood of living trees is liable to attack by various fungi which commonly gain access to it by means of wounds, due to abrasion of bark or the falling off of branches. The mischief is usually far advanced by the time the first symptoms are apparent, and it is often then too late to adopt remedial measures. In these matters "a stitch in time saves nine," and it is generally a simpler matter to clean and tar a wound at once so as to prevent the entrance of the disease-producing organism rather than to endeavour to extirpate it afterwards.

Some of these destructive fungi, instead of only attacking the dead tissues—the wood—of the trees, invade and kill the living cells. This is a more serious matter, for we must remember that only a very small part of a trunk is really alive in the strict sense of the word, that is, contains living protoplasm. Any pest which attacks the living tissues, and especially the cambium, often speedily kills it, or at any rate renders it practically worthless. Such fungi are those which produce the larch canker (*Dasyscypha Willkommii*) and the beech canker (*Nectria ditissima*), the latter being especially destructive to the cells of the cambial region and thus producing very dangerous lesions.

One of the most interesting of the tree diseases is that produced by the fungus known as *Armillaria mellea.* The fructifications are easily recognised as clusters of brown toadstool-like bodies which spring from the roots or stumps of dead trees at the ground level. Each "toadstool" is characterised by the possession of a ring or frill underneath the cap which bears the gills. Before its life history became known, and consequently methods could be devised to check its progress, the fungus was a very dangerous one, especially when it invaded the pine woods, for it spreads fairly rapidly from one tree to another. The mycelium grows in the cambial region, and also in the sapwood of the tree, but the special point of interest about this fungus lies in the circumstance that black cord-like mycelial strands are produced in the tree by the approximation of hyphæ, which then become woven into thin strands. These grow as organised structures, and some of them force their way out of the tree below the surface of the soil, there continuing to elongate till they reach the roots of other pines. They then enter these, and so the pest may easily assume the character of an epidemic, extending from one pine to another as from a centre, and killing the trees in its advance.

## CHAPTER XV

### FUNGAL PARASITES

The history of our cultivated plants, both in Europe and, to a far greater extent, in the tropics, bears abundant testimony to the magnitude of the evils caused by fungal enemies. The conditions under which crops are generally grown happen, unfortunately, to be specially favourable to the spread of infectious fungal disease. Diseases of this kind are apt very easily to get beyond control unless they can be checked in their early stages. Even with all our present precautions the annual loss from fungal disease is gigantic, amounting to many millions sterling in this country alone.

Regarded from a biological point of view, the parasitic species are in many respects the most interesting of the group of fungi. In spite of their simple structure we find their physiological properties are very much specialised, and admirably adapted to their particular habits as parasites. In these respects, however, they show wide differences in behaviour. Some ruthlessly kill their host, reducing it to a mass of rottenness—for instance, the Phytophthora, which is the cause of potato disease. Others, while taxing their host for their own means of support, make no excessive demands, and may even stimulate a locally increased growth on the part of their hosts, at any rate during the earlier stages of their development. Some of the rust fungi furnish examples of this, causing local thickenings on the stems of roses, nettles and other plants. A very striking instance of the influence that a parasite may exert on its host is afforded by a species of smut (*Ustilago violacea*) which sometimes infests the Red Campion (*Lychnis dioica*) of the hedgerows.

This species of Lychnis is a diœcious plant. That is to say, the flowers of some plants are exclusively female whilst the rest are exclusively male. The unisexual character is produced by the abortion of the pistil in the flowers of the male, and of the stamens in those of the female plants. The fungus only reaches maturity and produces its violet powdery spores in the stamens. So far as the male plants are concerned there is no difficulty, but with the female flowers it is otherwise. What the fungus does when it attacks the latter is to *stimulate the plant to produce stamens* exactly like those of a male flower. The mycelium grows sparsely in them until the pollen sacs are approaching maturity, then it suddenly breaks out into virulence and destroys the pollen-producing tissues, filling up the space with its own spores. Nor does the influence of this remarkable parasite stop here, for the pistil is arrested at an early stage of its development and in certain other structural characters the flower closely approximates to that characteristic of a male plant—so closely indeed that very careful experiments were needed to clear up the matter.

It is not known what the substance formed by the fungus, and responsible for the change, really is. All attempts to imitate its action, and to produce a similar result artificially have so far proved unsuccessful.

The somewhat common " witches'-brooms "

furnish another example of remarkable interference with the ordinary growth-processes of the host plant that a parasite is able to induce. The wild cherry trees are particularly subject to the attacks of a fungus (Exoascus) which fruits within the leaves and alters the boughs affected by it in a curious manner. They are much more freely branched, the leaves are often smaller and sometimes deformed, and flowers are seldom or never produced on the affected parts. Another kind of witches'-broom occurs on the fir trees in continental forests, though they are not so frequently seen in this country. It is produced by one of the rust fungi (*Æcidium elatinum*). A twig affected with it is a striking object, inasmuch as it grows up vertically on the bough instead of horizontally. This erect habit is maintained, and as the years pass the witches'-broom comes to resemble a little Christmas tree arising from an ordinary, horizontally-growing bough of the fir tree. Several kinds of firs are liable to the attacks of this fungus, but it is on the silver fir that the witches'-broom is most often seen.

Such relations between fungus and host as those just described, and many other examples might be added, very clearly prove that these apparently simple parasites are remarkably complicated from a physiological point of view. The surprising thing about them is their very accurate degree of specialisation to the hosts, by which they have been enabled easily to bring about these quite definite and characteristic changes of form. It is evident that the physiological adjustments must be very delicate, for all attempts to imitate them have so far ended in failure. But it is just on this quality that the more "educated" fungal parasites depend for their subsistence, and it is a quality which they share with other specialised vegetable parasites, as well as with the gall-producing animals.

It has already been said that all stages can be traced between a saprophytic and a parasitic habit as exemplified in the life histories of different fungi. Sometimes it is possible to trace the change from one to the other in a single individual. This may occur either by the fungus acquiring additional powers of attack or it may happen through a diminution of the power of resisting infection on the part of the victim.

As an example of the first of these we may select a common brown mould known as *Botrytis cinerea*. Like many of these fungi, Botrytis represents the mould form of one of the cup fungi (Peziza).

If the spores of the peziza fructification are sown on a living plant, say a carrot, they usually fail to infect it; but if they happen to fall on to a dead or decaying portion of the carrot, they grow and produce a mycelium which spreads through the dead tissues. And this mycelium can now invade the living plant. The hyphæ secrete a poison which kills the cells in advance of its track, and thus the fungus succeeds in completely destroying the plant. Critically regarded, the change from saprophytism to parasitism in this instance is a somewhat imperfect one because the fungus, inasmuch as it kills in advance, is really living on dead tissues. But it shares this property with the majority of the destructive parasites. It is only the more specialised forms that tax but do not destroy. It represents a transitional phase, and one of interest, inasmuch as it shows how appropriate nourishment may accelerate, and increase to an effective degree, physiological powers already present, but normally inadequate, for purposes of direct application.

As regards the susceptibility of the host plant to fungal attacks, it is a matter of the commonest experience that some individuals of a race are more liable to contract disease from these causes than others. Every year sees the introduction of new varieties of potatoes which are claimed to be immune towards the disease (Phytophthora) that often does so much damage to the crop. Sometimes these varieties are resistant in certain districts and less so in others, and it may happen that their immunity gradually disappears after some years of cultivation. It is evident, then, that immunity in such instances is not a simple matter. Whilst it may partially depend on those properties which together make up the "constitution" of a plant, it is also affected by the influence of surrounding conditions of life.

We know very little, as yet, about the nature of "constitutional" resistance. In some cases it depends on a well-developed epidermis, and on the absence of attractive substances, such as sugar, from parts of the plant readily accessible to the fungus. A curious example of immunity against rust fungi is furnished by some of the cereals recently raised at Cambridge. The fungus normally gains access to the interior of the leaf by the germ tube or hypha growing in by way of a stoma, and then attacking the living cells. But it is possible to find a wheat plant so sensitive to the influence of the fungus that the cells die immediately the hypha approaches them. The fungus is thus effectively starved, and is unable further to infect the plant. It may also happen that when a fungal hypha has entered a plant, the attacked and injured tissues are cut off from communication from the healthy ones by a layer of impervious cork, and in this way the further spread of the disease within the body of the plant is prevented.

The part played by the environment in increasing liability to infection depends on a number of possible factors, all of general biological interest. A close damp atmosphere is not only favourable to the germination of the fungus spore, but it may at the same time injuriously affect the development of the cuticle of the leaf. Or, again, it may lead to an excessive amount of watery sap in the superficial tissues, quite apart from the effects of external moisture on the outer surfaces of the stems and leaves. It is well known that bad cultural conditions may predispose plants to disease, and observation teaches that sometimes, at any rate, the effects are due to imperfect development of the tegumentary tissues.

The presence of nitrogenous manure in excessive quantities, in proportion, that is, to the other nutritive constituents of the soil, is another predisposing cause of fungal attack. It operates in several ways, but often indirectly by causing an undue accumulation of soluble nutritious substances in tissues and cells the walls of which are imperfectly thickened.

Starvation of an essential food constituent may act as a specific cause of predisposition. Thus many grasses, when they are grown on land in which the supply of potash salts is inadequate, become very liable to epidemic attacks of a fungus known as *Epichloë typhina*. The disease makes its appearance in the form of white (changing to yellow) zones situated just above the knots of the stem, and extending upwards for a centimeter or two. These zones mark the regions where the reproductive organs of the fungus are formed. A poor supply of potash is also known to affect the formation of carbohydrates in the plant. In other words, the predisposition to infection in this instance is probably connected with a disturbance of the photosynthetic processes.

The whole matter of immunity is evidently very closely related with nutrition. It may be the result either of a defective hereditary constitution or of some property of the environment (*e. g.* excessive or deficient supplies of essential food elements) which interferes with the chemical processes of the manufacture, distribution, or utilisation of food within the organism. The part played by the fungus depends on its physiological capability to take advantage of the host plant. It must be able to enter the body of its victim, and either utilise there whatever stores of nutriment are directly available, or it must modify the vital processes, and in this way secure for itself the nourishment it needs. Some of the extremely specialised parasites, and especially some of the rusts, are limited to particular species, and even subspecies, of plants as hosts. This can only be interpreted as meaning that they are adapted to live on a very special kind of food, and perhaps also that they are easily affected in a prejudicial manner by substances which occur in species nearly related to their own proper hosts. But even the specialised parasites are capable of further extending their range. For example, the Brome grasses, of which there are a number of species in Britain, are liable to the attacks of a parasitic rust fungus known as *Puccinia dispersa*. Now when the parasite has been growing for a while on one species of brome, it loses the power of infecting some of the others. And yet the puccinia is found flourishing on these apparently resistant species also. The clue to the puzzle lies in the fact that although the puccinia thus develops "races" which preferably attack single species of brome, they can be induced to recover their powers of infecting others by the simple device of cultivating them on other species which are only intermediate in their powers of resistance. Thus a race which will thrive on a species *A*, but cannot attack another species *C*, will nevertheless recover the power of doing so if it be grown on a third species *B*. This remarkable occurrence of "bridging species" of plants is of obvious importance in connection with the sudden appearance of parasitic epidemics. It is not confined to the rust fungus, but is known to extend to others; amongst them is *Erysiphe graminis*, which also infests the brome grasses

# CHAPTER XVI

## FLOWERING PARASITES

It has been already pointed out that the non-green saprophytes or parasites are by no means limited to the classes of Fungi and Bacteria. Quite a large number of the flowering plants have adopted the habit of utilising extraneous stores of organic food, and in connection therewith have more or less lost the faculty of producing chlorophyll. There is the strongest possible evidence that the change has come about in correlation with the altered conditions of nutrition. In other words, the more or less complex food-substances present in the living or dead bodies of other organisms do influence the structure of those plants which make use of them, and one result is seen in the loss of the faculty of producing chlorophyll.

One might, then, expect to find many links connecting the normal green plants with those highly specialised, or as they are often called, degraded, forms characteristic of extreme parasites. And as a matter of fact we can trace such a series in a number of instances.

The Mistletoe (*Viscum album*) is a parasite which betrays very little of the degeneration we often associate mentally with a parasitic habit, but it has nevertheless undergone considerable modification in its root structure, whilst there is little in its stems and leaves, or in the internal anatomy of these organs, to indicate its particular habit of life. The reason lies solely in the circumstance that it has in no way abandoned the functions of independent photosynthesis. It only withdraws water and inorganic salts from the host plant which it infests, but makes no demand upon it for sugars and other complex organic food. It is mainly in respect of its root system that it has become modified, for the machinery requisite for continual absorption of water from the wood of a living tree is very different from that which is adapted to discharge a similar function in the soil. Branching green structures, which probably represent creeping stems, traverse the rind of the tree on which the mistletoe is growing, and from these there grow peg-like protuberances which become firmly embedded in the wood. These pegs are the real mistletoe roots, and they are very carefully adjusted in the manner of their growth to the habits of the particular tree in which they occur. Their rate of elongation exactly coincides with that of the increase in thickness of the branch. It is, of course, only this accurate adjustment that renders it possible for the mistletoe to flourish at all, for it is clear that the roots would otherwise be unable to maintain that intimate connection with the wood of the tree which is necessary both to fix the parasite to its support and to draw from the host plant the supplies of water it requires for its own purposes.

There are other near relatives of the mistletoe, belonging to the genus Loranthus, which are far more dangerous and destructive parasites. These plants are common in the tropics, and they form leafy, bush-like growths in the trees they infest. Many of them bear beautiful trusses of red flowers, and they somewhat recall the appearance of fuchsia bushes perched among the trunks and boughs on the outskirts of the forest.

Like the mistletoe, it is the roots of a loranthus that have undergone important changes in relation to the parasitic habit. They arise as sucker-like outgrowths from special creeping stems of the loranthus which grow along the surface of the tree. As the sucker-bearing branches are freely produced, and may reach a considerable length, the parasite often does very serious damage.

It is not a little curious that in a large family of plants like the Loranthaceæ, to which both Loranthus and the mistletoe belong, some species should not have advanced still farther in the parasitic direction. But although nearly all of them draw their water supplies from another plant, they have never taken the final step of absorbing from it the organic food. They have consequently, or perhaps one should say correlatively, retained their leaves, and all the complexity of structure which, as we have seen, the presence of the green leaf entails.

The parasitic habit has appeared independently in a number of other families of flowering plants. In some of them it is characteristic of practically all the members, just as in the Loranthaceæ mentioned above. As a matter of fact, in very many of the larger natural orders or families we also find species which have more or less broken away from the ranks of typical green plants in connection with their assumption of saprophytic or parasitic habits. Sometimes we can construct, within the limits of nearly related groups, all the stages, starting from a sort of dalliance with robbery which is hardly betrayed by any essential structural change, but culminating in species which, so far as their vegetative structure is concerned, have lost all resemblance to the forms of higher plants.

Thus in the alliance or family to which the snapdragon belongs, the familiar little Eye-bright (Euphrasia), abundant on grassy downs, the pink Lousewort (Pedicularis) of the marshes, and the yellow Cow-wheat (Melampyrum) of the woods, all have begun to supplement the legitimate stock of food which they manufacture for themselves by stealing from adjacent plants. This they are enabled to do owing to the ability they possess of modifying certain rootlets to form suckers, which then become attached to, and penetrate the tissues of, the underground parts of neighbouring plants. Although they have thus taken a considerable step on the road to parasitism, they are still not very dependent on the advantage they have gained. They retain their green leaves, and they will often continue to grow even when there are no suitable hosts which they can attack.

There are other species, not very distantly related to the foregoing, which have advanced much further. The Broomrapes (Orobanche) consist of a number of species, each parasitic on some kind of flowering plant. One of the common species grows on the roots of the broom, but it betrays no obvious sign of its existence until the flowering shaft is formed. The vegetative part of the plant consists of a small tuberous mass which is closely adherent to the root of the broom from which, by means of its sucker-like roots, it derives the whole of its food. The bodily structure is simplified, and the broomrape consists of little more than a small underground tuber which produces a few specialised roots. It only shows itself above ground when the time comes for it to put forth its large and rapidly developing flowering shaft, on which are borne the reddish flowers and small brownish-yellow leaves. Its tiny seeds, like those of some other parasites, are remarkable in that they do not even begin to germinate unless they happen to lie in close proximity to the host of a plant which they can successfully attack. This striking peculiarity enables us to appreciate something of the remarkable qualities which render so specialised a parasitic habit feasible at all. For the parasite has evidently become sensitive to the presence of a definite substance which emanates from the host-root. The seed is then stimulated, and it awakes from its dormant condition. It germinates and its roots immediately grow towards, and penetrate, the plant from which it will ultimately draw practically the whole of its food.

A further state of simplification of vegetative structure is exhibited by *Rafflesia Arnoldii*, which is in many respects perhaps the most wonderful of all living flowering plants. It occurs in the Eastern tropics, and it produces the largest flower known, for it may attain to as much as a yard in diameter. The rafflesias are mostly parasitic on vine-like climbers (Cissus), and they pass their vegetative life entirely within the comparatively slender stems of their hosts. In this stage Rafflesia is extremely simple in structure, and indeed it resembles colourless fungal hyphæ more than anything else. The filamentous cells branch through the tissues of their host, and it is only when the period of flowering draws near that the parasite gives any sign of what is about to issue from the vine. The filamentous strands increase at the spot where a flower is to develop, and a sort of ball of tissue is formed which presently bursts through the rind of the Cissus stem. Presently the ball splits open, and there grows out from within it a flower bud which opens out into the single enormous blossom.

A more familiar flowering parasite is the Dodder. This plant infests various hosts, *e. g.* flax, clover, nettles, gorse, etc. It rather suggests in appearance bundles of pink string thrown at random over the vegetation. It belongs to the convolvulus family, and still more or less retains the twining habit so characteristic of many of its relatives. But whereas the leafy convolvulus merely supports itself by twining round its support, the almost leafless dodder puts forth suckers where its stem is in contact with that of its host, and from the central portion of each sucker a growth is formed which penetrates the plant. In this manner the dodder obtains the whole of its food, both water and organic substance.

Although the dodder is really little more than a specialised twining convolvulus, nevertheless, in relation to its parasitic habit, it has ceased to form green leaves, and it is not even rooted in the soil. It is true that when the seed first germinates it is anchored by hairs to the ground, but the lower part of the stem soon dies away, and the whole plant comes to be absolutely dependent on a parasitic life.

Nevertheless it has not wholly lost its chlorophyll, and it is of special interest to find that if it happens to grow where it cannot obtain plenty of nourishment from its host plant, a larger amount of chlorophyll can be formed; the stems, indeed, may even become distinctly green. Such an observation as this clearly indicates how closely the formative processes of a plant are bound up with its nutrition. But the extreme readiness with which the dodder responds to an appropriate stimulus, by the production of suckers, is shown by the fact that if one of the stems of the parasite happens to twine round another one, they commonly pierce one another with the suckers which are immediately produced at the places of contact.

# CHAPTER XVII

## COMPOUND ORGANISMS

It would be an error to imagine that all the flowering plants in which the production of chlorophyll is arrested are therefore to be regarded at once as parasites. We have already seen that vast numbers of the fungi feed on dead remains, rather than on living plants and animals. There are, likewise, many flowering plants which apparently behave in a similar manner and they are generally, on that account, classed as saprophytes. But, as we shall see, a closer examination of the facts indicates that many of them more nearly resemble the parasites after all, though the method of their parasitism is well concealed. The Bird's-nest Orchis furnishes an excellent illustration of this.

The bird's-nest orchis (Neottia, Fig. 21) is a fairly common, though frequently overlooked inhabitant of the humus soil of dense woodlands. It lives under the ground in the leaf mould, except when it pushes up its cluster of sickly looking flowers on a yellowish or brown stem in early summer. No green leaves are produced, though the flowering shaft bears rather large brown ones. Hence the plant is unable to manufacture carbohydrate food for itself in the way that its green relatives can do. Traced below the soil, the flowering stalk is seen to spring from a short, stumpy root-stock from which arises a huddled crowd of short, brittle roots.

The special interest of the bird's-nest orchis in the present connection centres in these roots, for it is through them that, somehow or other, the stores of food locked up in the humus soil are absorbed by the

Fig. 21.—*Neottia Nidus-avis*, a saprophytic orchid.

plant. Microscopic examination of a root shows that they are permeated by *fungal hyphæ*, and careful experiments have proved that it is through the intermediation of these fungal threads that the saprophyte chiefly obtains its food. It thus appears that the term saprophyte is not a very happy one as applied to a plant like Neottia. The relation is rather more akin to parasitism, and it is the fungus from which nourishment is finally extorted. But inasmuch as the root both houses the fungus, and also contributes something towards its support, the parasitism is not very one-sided, although the final balance lies with the flowering plant.

This association of the root with a fungus is a very intimate one in a large number of instances, and it occurs in a very great number of plants which would never be suspected of parasitic habits. The fungus-root is often called a *mycorhiza*, and it is worth while to study it a little more closely.

The roots of many of our forest trees produce few or no root-hairs. Instead of this they are closely invested with a hairy coating of fungal hyphæ. Not only do these hyphæ ramify in the soil, but they also enter the root itself. Sometimes, as in the pines, they only pass *between* the cells, and do not enter them, but in other cases, as for example in orchids generally, they *pierce* the cell walls and enter the living cells. In both of these types of mycorhiza the fungus is doubtless attracted to the root by substances which have a food value for its hyphæ, just as parasitic fungi are induced to enter the bodies of their victims. But in a mycorhizal association the cells of the root control the degree of invasiveness which the fungus can manifest, and not only so, but they often proceed to actually digest the fungus itself after it has flourished within them, and at their expense for a while.

We have here, then, a beautiful example of two-sided parasitism, in which the final balance of profit very clearly lies with the flowering plant. It is practically certain that the fungus obtains some carbohydrate food, at first at any rate, but in return for this the plant acquires mineral substances in solution, which the fungus absorbs from the soil. A considerable number of flowering plants are unable to thrive unless their roots become infected in this way. This is especially true of orchids. Indeed, one of the great difficulties experienced in raising these plants from seed has been solved by supplying the young seedling, during its germination, with the fungus appropriate to it. And so close has the degree of association between fungus and flowering plant become, both in orchids and in many other plants, that neither can grow properly in the absence of the other.

Now this intimate mycorhizal relationship is found to exist in all the flowering saprophytes, and it is reasonable to conclude that the loss of the green leaves and all the structural change consequent on their abortion is directly connected with the growing ability of the saprophytic plants to develop the physiological faculty of utilising the resources thus rendered available. They come more and more to depend exclusively on the nutritive processes of fungi, not only for their carbohydrate kind of food but for the still more complex nitrogenous nutriment as well. Of course, the decaying leaves and other vegetable matter in the soil maintain a plentiful and practically continuous supply of carbonaceous food which is constantly at the disposal of those organisms which are adapted to make use of it. There is little doubt also that during the decomposition of the carbonaceous humus free nitrogen is sometimes forced into combination with other elements, either by micro-organisms, or mycorhiza, or both, and so is rendered available for the higher plants.

This way of looking at the matter fits in with the very remarkable nutritive processes so characteristic of the leguminous plants of which the peas and clovers are representative examples. If one of these plants be dug up (Fig. 22), its roots will be seen to bear nodular, or wart-like, swellings. These swellings are due to luxuriant growth of the tissues of the cortex or rind. Examined microscopically the cells are found to contain enormous numbers of bacteria-like organisms to which the name of *Bacillus radicola* has been given.

The root becomes infected by this bacillus

Fig. 22.—Root tubercles on the roots of the Kidney-bean plant.

from the soil, in ordinary samples of which it is apparently always present. The bacillus enters through a root-hair, and when it reaches the interior of the cortex it multiplies there, producing the nodular outgrowths in question. It feeds and grows mainly at the expense of the sugars and other substances supplied by the host plant, these having, of course, been produced as the result of the photosynthetic activity of its leaves.

But when thus provided with carbohydrate food, the bacillus is able to manufacture the essential nitrogenous compounds necessary for the production of protoplasm by utilising the *free nitrogen of the air.* Most plants have to take in their nitrogen in a combined form, as ammonia salts, nitrates, etc., for nitrogen is a very inert element, and difficult to force into combination with others. *Bacillus radicola* is one of the very few organisms which can perform this really stupendous task, provided that it is supplied with the means of obtaining the energy required for the process in the form of appropriate carbohydrate nutrition. There is no doubt as to the facts, for the bacillus will do the same thing when cultivated outside the body of the plant, and under the most rigidly controlled experimental conditions.

After the bacilli have thriven for a while, mainly at the expense of the food supplied by the root in which they are living and multiplying, a change comes over them. Many of the individuals become weaker, and undergo a sort of degeneration, whilst a few pass into a resting stage in which they become highly resistant to adverse conditions of life. The leguminous plant, which hitherto has been paying out carbohydrate food to the bacillus, now begins to receive, and the harvest is a rich one, for it acquires from the degenerating mass of bacilli the stores of nitrogenous matter they have accumulated, and this affords a very good return for the sugars, etc., which it had previously expended.

The comparatively few surviving bacilli serve to infect the soil, as the roots gradually rot, and they thus are enabled to attack the roots of new leguminous plants with which they may be brought into contact.

In comparing the leguminous plants with the saprophytes and parasites that have undergone simplification (or " degeneration ") of vegetative structure we can readily understand why they have not lost their green leaves, and all that the possession of green leaves entails. For a continuous supply of carbohydrate is essential for the growth of the bacilli, and without it there is no manufacture of nitrogenous substance from the free nitrogen of the air. Moreover, the Leguminosæ have by no means abandoned the absorption of nitrates from the soil. The combined nitrogen they acquire from the bacilli is, for most of them at all events, rather of the nature of an additional supply, though it will, and often does, enable them to thrive under conditions of nitrogen starvation which would be fatal to the majority of other plants. Ultimately, however, they owe their faculty of "fixing" free nitrogen to the energy which the chlorophyll enables them to obtain from the sunlight. This is the motive power which enables the machinery of the green leaf to maintain its output of carbohydrate, and it is from this carbohydrate that the power or energy is more immediately derived which enables the bacillus to perform the tremendous operation of forcing free nitrogen into combination, and thus to build up from the raw materials the stuff from which protoplasm itself can be made. Although the leguminous root ultimately profits by its relations with the bacillus in thus acquiring a costly food in exchange for a cheap one, there is no indication of any degeneration of leaf structure on the part of the flowering plant. It even becomes almost unthinkable that it could occur, inasmuch as the continuous supply of carbohydrate from the green parts is a prime condition of the nitrogenous synthesis. The importance to the organic world of these plants which bring nitrogen into combination in a form that can be utilised by living beings is overwhelming. For apart from some means of maintaining the supplies of nitrogenous food, life itself would ultimately cease to be possible in the world.

There are many other instances of remarkable associations of two or more plants, in which each is in turn more or less parasitic on the other, or, at the least, lives on the waste products formed as the result of the chemical life processes of its associate. Such an association is often spoken of as symbiosis, but it is evident that the transition from symbiosis to parasitism is only a matter of degree. An excellent example of symbiosis is furnished by Lichens. These plants are compound organisms, made up of a fungus on the one hand, and a green alga on the other. It is often possible to separate the two, and to cultivate them apart, and the habit of growth (except in the most primitive forms) is very different from that which occurs when they associate to form the lichen. Lichens are formed in countless numbers every spring, and scrapings from the bark of damp trees at this season will generally yield quite a large selection of these compounded organisms in the making. Sometimes a particular fungus filament which comes in contact with an appropriate alga may be seen to branch and then to embrace the alga within its threads. Many of these early beginnings of lichens are really due to the escape, from older lichens, of algal cells, each of which is already accompanied by a few fungal hyphæ. These young associations—called soredia—may be recognised as the green or grey powdery dust which often occurs on lichens when in vigorous growth.

It is possible to make a lichen artificially, by bringing together the alga and fungus. And we learn that one fungus may attach itself to several kinds of algæ, and *vice versa.* In every instance, however, a specific lichen results from the union of a definite fungus with a particular alga—if either the alga or fungus be changed, a correspondingly different "species" of lichen is formed.

Both organisms thrive. The algal cells often become unusually large, and the fungal mycelium is evidently well nourished. But multiplication of cells and consequent growth is often greatly modified, especially in the more specialised lichens in which the two organisms become more intimately dependent on each other.

The symbiosis only continues to pay as long as the alga is properly exposed to light, and for so long as it is properly supplied with water, together with the small amount of mineral food it requires. The latter offices are largely discharged by the fungus, which usually attaches the lichen to the substratum, whilst its gelatinous walls retain the water supplies derived from intermittent showers or other sources. Thus a remarkable degree of correlation is displayed in the growth processes of the specialised lichens, and some of them simulate to a wonderful extent the form, and partly even the structural arrangements, to be met with in the green leafy shoots of higher plants (Figs. 23A and B).

Lichens are particularly instructive in showing that the form assumed by an organism is in the long run determined by the chemical reactions that have gone on and are still going on within it. These reactions are nicely adjusted, and are readily interfered with or encouraged by the conditions under which they take place. The result is perceived in a delicate adjustment of growth whereby the different parts are so correlated to each other that excessive development of one part carries with it its own order of arrest, whilst deflection of nutrition to or from any part will, of course, correspondingly affect growth in that region.

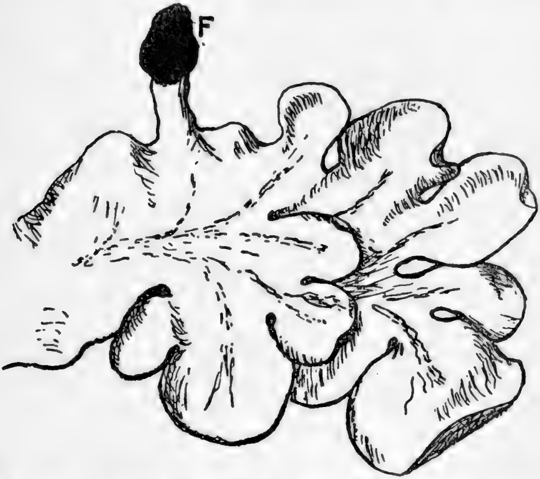

Fig. 23A.—*Peltigera canina*, a lichen. F, the fructification.

But, nevertheless, the parts of which the compound organism is made up largely determine the broad lines of possible development. If we alter the species, whether of alga or of fungus, we have seen that we correspondingly affect the " species " of lichen, as determined and defined by its own peculiar form and properties—*i. e.* its process of development.

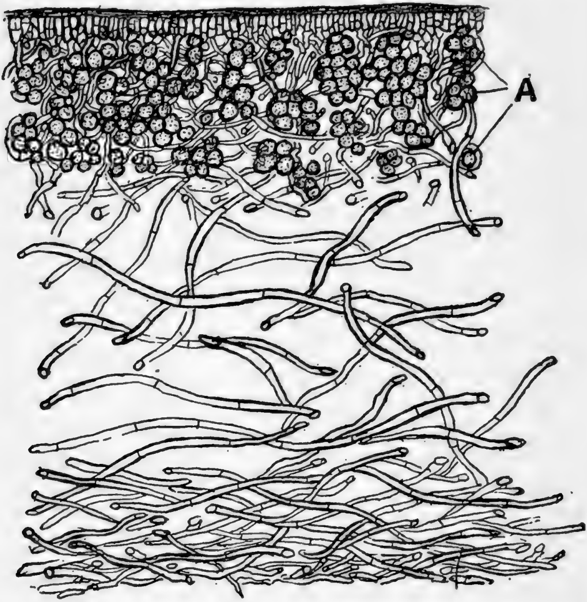

Fig. 23B.—Transverse section through the thallus or frond of a lichen (*Peltigera canina*). A, algal cells.

Of course, the combinations which are

encountered in nature are just those which are fitted for actual environmental conditions. Plants not so adapted are unable permanently to occupy any position at all. The positively unfit are speedily exterminated, and only those combinations which give good results can persist. But the "good results" are primarily the result of particular operation of internal factors. They arise as the inevitable consequence of the particular algal and fungal combination, and they are quite independent and irrespective of *ultimate adaptation* to light or other external conditions. These external conditions are the tests which largely determine not the *origin,* but the *persistence* (or extinction) of each and every individual sort of lichen.

It may not be possible to push very far our analysis of the factors involved in the genesis of form and structure on the one hand, and those correlations of growth wherein so many "adaptive modifications" consists on the other. It may well be, however, that an experimental study of lichens is destined to throw light on much that is now obscure. For in witnessing the synthesis of a lichen, and the modification in structure and habit which results from the association of the two symbionts, we seem to have caught a glimpse of the secret methods and processes which direct the evolution of organic form.

# CHAPTER XVIII

## VEGETATIVE REPRODUCTION

Reproduction, in its simplest and most primitive form, is one of the most obvious results of growth. It represents, after a fashion, and in a certain tangible form, the balance of profit over expenditure on the part of the individual, which is applied to the extension of the business of the species or race. But the process is not a simple one. When a unicellular plant, Chlamydomonas for example, has reached a certain size, the protoplasm ceases to grow. It divides, and the products of this fission, which may be repeated several times, separate from each other as new and independent individuals. Nothing is left of the old organism, it has simply split up into a number of smaller ones. In other words, the nutritional processes which enabled growth to proceed have prepared the way for, and have then given way to, a new set of chemical processes, and these result in the cleavage of the mass into smaller parts. This cleavage, or cell-multiplication, may be started in several different ways, but the method most often encountered in nature clearly depends on factors which are themselves more or less intimately connected with an abundant supply of nutrition.

The rapidity with which many of these simple plants can multiply, provided the nutrition conditions are favourable, is truly astonishing. Instances are not uncommon, especially among bacteria, in which a cell colony will double its numbers every twenty minutes or so. That is to say, in about twelve hours one cell might give rise to nearly seventy thousand million cells. It is highly improbable that anything approaching this number would actually be reached, because as the colony begins to grow the individuals composing it compete with each other for the food supply, and those more centrally situated will obviously be at a disadvantage in this respect. Many other conditions, also depending on the crowding of the cells, will begin to make their effects felt on the reproductive capacity of the members of different portions of the colony.

Now what is true of a colony of detached individuals is still more applicable as soon as the dividing cells cease to separate at once from each other. This naturally follows from the simple geometrical fact that if the cells are all growing and dividing equally and in all directions, the surface of the cell colony only increases as the square of the radius of the growing spherical mass, whilst its mass increases as the cube. The difference in available nutrition evidently must affect the growth of individual cells, and hence the shape of the colony as a whole. Doubtless the elongated, narrow cylindrical form of fungal hyphæ is to be interpreted, in part at any rate, as an expression of this fact. Vegetative reproduction tends, in such forms, to occur by the transverse fission of the cylindrical growths; but, as we have already seen, multiplicative processes are not identical with those of growth, and both in the fungi and in other lowly plants, nutrition sets other processes in action which lead to the formation of various sorts of specialised reproductive cells. This does not, however, interfere with the ordinary multiplication by fission, which still remains as a common feature among them.

In the evolution of the more complex plants, the cells—the primitive individuals—become organised into a higher individuality. The sense in which we use the term reproduction gradually and insensibly changes, and we distinguish between *cellular multiplication* and the *reproduction* of the multicellular individual. We may still think of the multiplication of cells as reproduction in the abstract, but our unit organism, so to speak, has become transformed; it is no longer identical with the isolated cell, but is represented by the cell colony. Reproduction in such a colony, concretely considered, comes then to signify the process by which, not new *cells* only, but new *colonies* are started. It is a change in the point of view.

The most common method by which the simpler aquatic algæ reproduce themselves vegetatively is by giving birth to *zoospores.* The protoplasmic contents of a cell contract away from the wall, cilia are developed, and the zoospore escapes through a hole which is formed in the cell wall. Very often a series of adjacent cells may be seen all to give rise to zoospores in this way. Sometimes the zoospores are not so simple, and represent not single cells only but a cluster, the individuals of which are not delimited by walls from each other. The huge zoospore of Vaucheria belongs to this type; it is easily visible to the naked eye, as it rolls about through the water by means of its numerous pairs of cilia.

But however the zoospores are formed, they generally settle down after a period of independent movement. They withdraw their cilia, secrete a cell wall over their naked surface, and grow into an organism generally similar to that from which they themselves have sprung.

It is different with land plants. Motile propagative bodies would be practically useless here, and the nakedness of the protoplasm would render them specially susceptible to numerous adverse influences inseparable from existence on land. In the simpler forms we find that entire cells, *i. e.* protoplasts which remain enclosed in cellulose membranes, replace the naked zoospore. From this simple stage the rest is easy. A few coherent cells become detached as a sort of bud or gemma, and so reproduce the parent plant. Mosses and liverworts are freely reproduced in this manner. The gemmæ are of all shapes and sizes. They may be produced in a variety of ways, *e. g.* as biscuit-like outgrowths from the leaves, and sometimes, as in the moss Tetraphis, the whole of the leaves at the growing point of older stems may develop into reproductive bodies of this kind. Propagative outgrowths may also occur on the underground parts of the stems of mosses and liverworts, and they are often filled with reserves of food. Thus they enable the species to tide over periods of drought, etc., which might easily prove fatal to the individual. On the return of better conditions they sprout, and thus reproduce the plant afresh.

Passing to the higher plants, the vegetative propagative processes are seen to exhibit almost infinite variety. The smallest parts of some plants are capable of reproducing the whole—as any one may discover who endeavours to eradicate troublesome weeds, *e. g.* bindweed, from a garden. The regular storage organs, bulbs, tubers, etc., are specially fitted to serve as propagative organs on account of the stock of organic food they contain. Bulbs, for example, consisting of a short squat stem bearing fleshy leaves, form the ordinary propagative bodies of lilies. Even a single scale, detached from the bulb and planted in soil, will commonly give rise to new plants, and this faculty is taken advantage of in propagating new and valuable species.

Sometimes young plantlets are produced by the development of a cluster of cells which still remains attached to the parent plant. This happens in many ferns, where bulbils are formed on the leaves or leaf stalks, and when they are set free they are already provided with all the organs necessary to start at once into growth. The process of propagation by gemmæ and by young plantlets is essentially the same, the difference consists in the particular stage of development which is reached when the propagative body is cast adrift from the parent. The gemma is shed at an early stage, while the bulbil represents a gemma that has remained to develop on the parent plant, and has been fed at its expense during the early stages of growth. But there are advantages and disadvantages in both methods. The gemmæ are small, and are more readily dispersed over wide distances than the larger young plants. Furthermore, the latter by their very complexity are more liable to perish unless they speedily reach a spot in which they find conditions suitable for immediate development.

But in spite of these numerous and elaborate kinds of vegetative reproduction, most plants still retain the primitive capacity of merely regenerating lost parts to a surprising extent, a circumstance of which advantage is taken in the propagation of valued species and varieties. Everybody knows how simple it often is to increase a plant by cuttings. Sometimes cuttings of roots will grow just as easily as those of stems, and even the leaves of some plants may be used with almost certain chances of success. Begonias, for example, and certain other greenhouse plants, are generally propagated in this way.

Again, in the operations of budding and grafting, we see how the process of cell division and multiplication is followed by cohesion; the bud or the graft "takes," becomes united with the tissues of the stock. Instead of the bud or cutting being planted in the soil, it is here planted on to another organism. And, in passing, we may note that the graft produces no roots, as it would have done if planted in the soil. The internal stimulus which might have led to root production is absent, inhibited, perhaps, by the nutrition that is plentifully poured in from the tissues of the plant on which the bud or graft is growing.

All the various examples of multiplication and propagation to which allusion has been made in this chapter are instances of what may best be called *vegetative* reproduction or propagation, and they are seen to be intimately related with the functions of growth and nutrition. They represent various methods of dividing up the individual, and the liberated portions grow up into plants like those from which they have themselves been derived. From simple beginnings the propagative bodies advance in complexity, and other structures, not in the first instance differentiated as propagative bodies (*e. g.* thickened stems in which food is stored), easily assume this function of vegetative reproduction. One may often trace the stages by which this is brought about within the limits of a group of closely related species. The Jerusalem Artichoke, a sort of sunflower, is connected by all imaginable transitions with other species in which the underground stems have not yet proceeded to form tubers (as in the artichoke), but exist as mere whip-like runners which turn up and only grow to new plants by the slow and accidental process of rotting off their connection with the parent plant. In others the propagative character is still less evident, and the storage function is absent altogether. Finally, there are many sunflowers which normally fail to produce any underground runners at all.

Thus, in spite of the endless variety in the carrying out of the process, the essential character of vegetative propagation is really a simple one. In this respect it stands in marked contrast to the other, the sexual, reproductive process, which will form the subject of the next chapter.

# CHAPTER XIX

## SEXUAL REPRODUCTION

SEXUAL reproduction occurs in almost all the divisions of the animal and vegetable kingdoms, although it has not as yet been detected in some of the lower groups. These consist either of organisms of extreme simplicity, or of those in which we have grounds for believing that sexuality has been lost, probably in connection with special conditions of nutrition. In some of the higher plants the sexual function has degenerated, though we cannot clearly trace the loss to any definite cause.

The most striking peculiarity connected with sexual reproduction, next to its almost universal occurrence, lies in its remarkably complex character. Moreover, its effects on the development of the vegetable kingdom have been extremely far-reaching, and have profoundly influenced the direction of evolutionary progress, as interpreted by a study of the life-history of the plants themselves.

The sexual act itself stands in strong antithesis to vegetative propagation, for it does not directly involve an increase, but a reduction in the number of cells. Two cells, which we may call the *gametes*, are concerned in the process, and they invariably coalesce to form one—the *zygote*.

From the zygote, which is always a single cell, there springs a new generation which may multiply in various ways, but sooner or later a process supervenes which leads once more to the formation of new gametes. These in their turn may coalesce in appropriate pairs and so form new zygotes.

In the more primitive unicellular plants the sexual cells or gametes are often apparently precisely similar to each other. They may also be externally indistinguishable from the ordinary vegetative organism itself, or at any rate from the newly formed individuals which have just arisen by vegetative propagation. Nevertheless the sexual individuals are physiologically very distinct. If it were not so, they would scarcely be definitely impelled to unite, and to unite only in pairs.

Closer examination reveals the fact that in sexual union the coalescence of the gametes is a very intimate one. Not only do the extra-nuclear protoplasms flow together, but the two nuclei also unite and mingle their contents in common. A study of the higher types, both of animals and plants, leads to the further conclusion that it is in the nuclear fusion, more than in anything else, that the significance of the sexual act is to be sought. We shall return to this point later, but it will be convenient and profitable in the first place to glance at a few examples, in order to gain some knowledge of the general character of the sexual process itself so far as we at present understand it. At the same time, we shall be in a better position to appreciate the bearings of its elaboration on the evolution of the series of higher plants.

If we once more take as our starting-point a relatively simple unicellular plant such as Chlamydomonas, we find that under certain conditions it continues to grow and to multiply itself vegetatively (see p. 15). After a time, however, and under certain altered nutritive conditions, sexual reproduction sets in (Fig. 24). The young individuals which have been recently liberated from parent cells, after swimming about for a while, undergo a change. The living protoplasmic body slips out of the cellulose skin, and swims as a naked cell in the water. Very soon these cells are observed to approach one another in pairs. Two individuals become attached, and then gradually coalesce. The cilia disappear, and the now motionless zygote becomes spherical and surrounds itself with a new cell wall. Chemical changes continue to go on within its body, for the chlorophyll loses its green colour and gives way to a red pigment. Later on, and after a longer or shorter period of rest, the green colour returns, the cell reawakens to vegetative activity, its contents divide, and new chlamydomonas individuals are produced.

Now the chlamydomonas is an especially interesting organism inasmuch as it responds

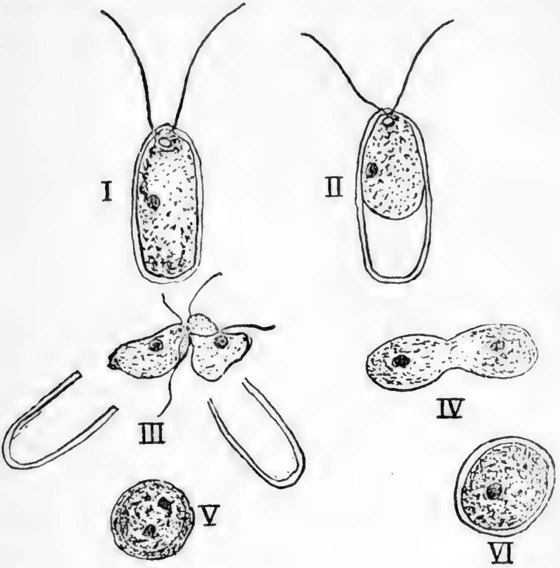

Fig. 24.—*Chlamydomonas media*, sexual process. I.—Sexual cell (gamete). II.—The same, somewhat more advanced. III.—The protoplasts, which have escaped from their cellulose membranes, just in contact. IV.—The fusion nearly complete, note the two nuclei (dark spots), one in each gamete. V.—Complete protoplasmic fusion of two gametes, but the two nuclei still distinct. VI.—The zygote after complete fusion, surrounded by a new membrane.

with great precision to various changes in external conditions which are able to influence its nutrition. It is possible to maintain the plant, apparently for an indefinite period, in a state of vegetatively active growth. On the other hand, it may with almost equal certainty be compelled to enter on the sexually reproductive phase of its life. A sudden starvation, if previously well nourished, and so long as the organisms are exposed to light, will at once bring about the change that leads to the formation of gametes. But we may at once confess that we do not as yet understand how these conditions work in producing the observed effects. Nor are we able to form a clear idea as to why the addition of nutritive salts to the water in which the chlamydomonas is living suffices at once to arrest sexual development, and to switch the life processes back on to the vegetative course; so much so, indeed, that even gametes can develop independently, and in a vegetative manner, *i. e.* without any sexual union.

But the effects of sudden starvation on previously well-nourished organisms are well known to conduce to the development of sexual reproductive organs. In a chlamydomonas the organism and the sexual cell are practically identical, and it is in the highest degree suggestive to find that what stimulates the production of sexual organs in a complex and highly differentiated plant will also cause the undifferentiated primitive one also to enter on a sexual condition or phase. Moreover, the converse is also true, though it is often less easily demonstrated. For a reversal of the conditions that led to the development of the sexual state will arrest it, and cause not only lowly, but many of the higher plants to resume their vegetative growth. Some of the malformations often seen in flowering plants, as the consequence of injudicious manuring, represent the results of the antagonism between the sexual and vegetative functions.

But in the more specialised plants, where the sexual and other reproductive cells are different from the general mass of the body cells, the sexual elements themselves are more limited in their range of development. We can, in favourable instances, so influence the *plant* as to determine whether or not it shall form sexual organs. But where once the sexual cells are formed, *these* can seldom be induced to develop further, unless they unite in appropriate pairs. For some reason the chemical processes no longer run in the direction of growth and development. They result in death and disintegration unless a sexual fusion occurs.

We do not as yet know why this should be so, but the experimental work of recent years has taught us that by suitably altering the conditions of chemical action within the protoplasm of the gamete, and especially by appropriately regulating the oxidative processes, the cell will again be able to resume vegetative activity. Loeb and others have shown this to be experimentally possible with eggs of various animals; and although it has not yet been satisfactorily demonstrated in plants, this is largely owing to the very small size of the egg, and to its ordinary inaccessibility for purposes of this kind of experiment. There is no doubt that the essential processes are identical in animals and plants, and, moreover, we are aware of instances amongst the latter in which eggs can be stimulated, though by indirect means, to grow and develop in the absence of fertilisation.

We do not as yet at all understand—and yet this lies very near to the root of the whole matter—why the sexual change should produce two kinds of states. We speak of these states as male and female respectively in the higher forms, but there is no detectable difference between the gametes of the simplest organisms. Why there should be this difference of state, and why the coalescence of two individuals should not only obliterate it, but give special vigour to the resulting cell we are not as yet in a position to declare.

As we pass from the lower to the higher ranks of the vegetable kingdom, we find that the primary physiological differences by which sex is first differentiated are betrayed by secondary changes which enable the male to be distinguished from the female gamete. The general trend of the distinction is unmistakable, and is of considerable importance in its connection with the sexual act. The chief character which urges itself on our notice consists in the relatively large size of the egg or female gamete, and the small size of the other, the male or sperm.

The egg not only becomes large, but it loses the power of independent motility. It consists of a bulky mass of cytoplasm, in which nutritive matter is often present, and it also contains a large and somewhat watery-looking nucleus.

The sperm, on the other hand, is small and compact. It is nearly always actively motile, though this character is almost or entirely abandoned in certain groups, such as the highest flowering plants in which this has evidently occurred as the result of correlation with other secondary changes connected with pollination, which render motility useless or even disadvantageous. In another important respect the sperm also differs from the egg, inasmuch as it tends to become composed almost entirely of the cell nucleus, the cytoplasm being merely represented by the cilia and a thin skin which sheaths the nucleus as a whole.

One of the results secured by fertilisation has already been pointed out, namely, the vigorous development so characteristic of the sexually produced organism. But there is another and perhaps hardly less important consequence, namely, that the zygote combines within itself the slightly different properties borne by the egg and sperm, in so far as they are of different origin. This must be specially true when the gametes spring from different parents, for there is no doubt as to the transference, by means of the gametes, of the hereditary qualities of the organisms from which the gametes have sprung.

Experience teaches us that the egg and sperm contribute equally towards the characters of the plant which will develop from the zygote. The reason for this almost certainly lies in the preponderant share taken by the nucleus in determining the organisation of the individual. The sperm and egg contain about equal parts of the essential constituents of the nucleus, and this explains the circumstance that the minute sperm is as potent, from the point of view of the transmission of hereditary characters, as is the bulky egg.

These two functions, rejuvenescence and the combination of diverse hereditary characters, then, are the most obvious results achieved by fertilisation. Probably the first-named function, rejuvenescence, is the more primitive, and the chemical affinity between the egg and sperm first arose and was maintained by the primitive conditions that made fertilisation a *conditio sine quâ non* of further development. But the second was inevitably bound up with it. This latter circumstance was fraught with tremendous consequences which were destined to influence the course of evolution of the entire organic world, of animals no less than plants.

One of the most singular features of the sexual act, in so far as it can be actually observed, consists in the attraction which the gametes exercise on each other. It is by this means that fertilisation is rendered possible, and is definitely secured.

As the differentiation of the male and female gametes becomes more pronounced, the immobile egg is ardently sought by the motile sperms, and the latter are evidently stimulated by something which emanates from the egg. Even when the sperms are not themselves vigorously motile, they are often, as in the case of the flowering plants, conducted to the egg in an analogous, though more indirect, method in which attraction plays a part. For the pollen tube, in which the male gametes are contained, grows into the cavity of the ovary, and thence to the ovule in which the egg is formed, and it there discharges them in such a way as to render fertilisation almost inevitable.

But it is simpler to choose a less specialised type than the flowering plant in order to become familiar with the essential facts of fertilisation. For this purpose some of the brown seaweeds (Fucus) afford admirable material. They produce large quantities of eggs and sperms in little conceptacles situated near the tips of the fronds. The eggs and sperms are extruded from the conceptacles into the sea-water, and the sperms are soon observed to be actively swimming in all directions. At first the eggs exercise no influence upon them, but as the membranes, in which they are at first enveloped, dissolve in the water, the sperms are seen to cluster around the eggs, and each egg becomes the centre of a crowd of male gametes which are endeavouring to gain entrance into its substance. Presently one slips through the peripheral limiting pellicle of the protoplasm and gains the interior of the egg. It passes rapidly through the cytoplasm and becomes appressed to the egg-nucleus. In a few seconds it swells up, and finally the two nuclei, belonging to the egg and sperm respectively, coalesce, and fertilisation is thus achieved.

Now it is a remarkable fact that during fertilisation only *one* sperm is required to fertilise the relatively large egg. This is true of animals as well as plants. Experiments have clearly proved that normally only one male cell can enter the egg at all, and that in any case only one male *nucleus* fuses with the egg nucleus. The study of seaweeds has furnished a clue to the means by which the entrance into the egg of but one of the crowd of struggling sperms is effected. It has also thrown light on some important features of fertilisation itself.

Certain seaweeds (Halidrys) have very large

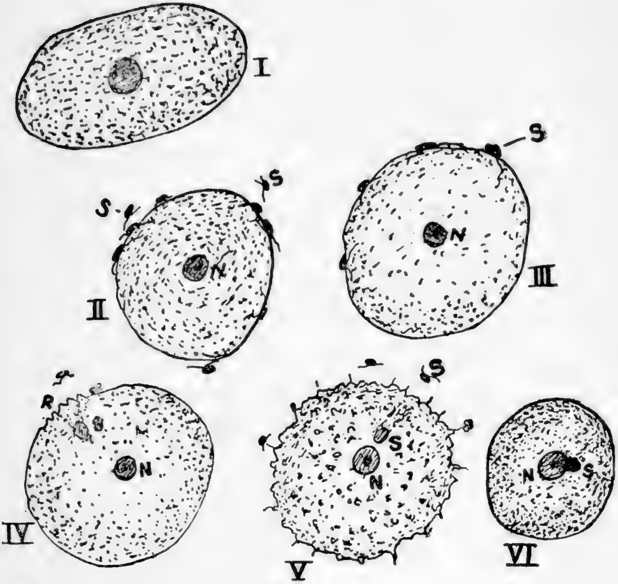

Fig. 25.—Fertilisation of *Halidrys siliquosa*. I.—Egg when first extruded into the sea-water. II.—Later stage, egg spherical. III.—Egg suddenly enlarged, just before fertilisation. IV.—Fertilisation. The sperm (S) has slipped in at the "crinkled" spot (R). V.—After fertilisation the egg becomes crinkled all over and no longer attractive, but poisonous to sperms. VI.—The fertilised egg has contracted and is surrounded by a newly formed membrane.

eggs, and if they are kept in sea-water as they are extruded from the conceptacles, and are watched under the microscope while the sperms are swimming about them, they will be seen, one by one, suddenly to change their form—they swell up, and at some one spot on their surface they become "prickly." This prickliness spreads with great rapidity over the surface of the egg. The onset of this curious appearance marks the entrance of a sperm into the egg. The immediate effect of that sperm on the egg protoplasm is to render it not only no longer attractive to the rest of the sperms, but actually poisonous to them. An explanation is therefore at once furnished as to how the entrance of more than one sperm is prevented. The change is a sudden one, resulting from the interaction of the substance of the egg and sperm—a circumstance which sufficiently emphasises the physiological difference existing between them. Under unfavourable conditions, *e. g.* badly aërated water, or by the addition of certain substances to the water, the suddenness of this reaction can be slowed down, and then it may happen that more than one sperm effects an entrance. But it seems to be a general rule that if more than one of them fuses with the *nucleus* of the egg, either no further development takes place, or monstrous embryos are produced which commonly die during the earlier stages of development.

It is evident, then, that the act of sexual fusion produces striking and immediate change in the egg, and that the fusion of the two *nuclei* is an essential part of the whole process.

The result of fertilisation is invariably to start a series of chemical changes in the egg. The first of these changes commonly results in the secretion of a membrane over its outer surface, and then a period of quiescence usually intervenes before any further visible development begins. After the lapse of a certain time, which may vary within rather wide limits, the fertilised egg commences to "develop."

The lines along which development proceeds differ greatly in different groups of plants. In the simpler ones, such as Chlamydomonas, no apparent growth takes place, but the zygote divides, giving rise to a number of separate cells which escape as zoospores from the zygote membrane, and finally grow into as many different individuals. A somewhat similar course is pursued by many other algæ, but in some of them the production of motile zoospores is postponed until after an embryo, composed of a larger or smaller number of cells, has been formed.

In the higher plants, from the mosses upwards, the zygote gives rise to a plant quite unlike that from which the gametes were produced. This plant forms reproductive bodies known as spores, and when the spores in their turn germinate, they give rise to another very dissimilar cellular structure, the prothallus, on which the gametes are ultimately produced.

It is, however, impossible to appreciate the significance of all this without some preliminary acquaintance with the behaviour of the cell nucleus, and its relation to cell division and cell organisation, which will form the subject of the following chapter.

## CHAPTER XX

### THE CELL-NUCLEUS AND FERTILISATION

In order to be in a position to grasp the essential facts of fertilisation, and their far-reaching consequences on the organism in general, it is necessary, as stated in the concluding paragraph of the preceding chapter, to learn something of the structure of the nucleus. Moreover, a study of the nuclear processes will enable us to apprehend the meaning of some of the most constant and singular features which, in the form of alternation of generations, are of such widespread occurrence in the vegetable kingdom.

The nucleus is perhaps the most important organ of the cell. There are strong grounds for believing that it is largely concerned in the determination of those hereditary qualities which distinguish one species from another; and we are also well aware of its great importance in governing the chemical changes which proceed within the protoplasm.

The nucleus consists, essentially, of a variety of substances, more or less gelatinous in consistency. These, together with more fluid constituents, are contained within a membrane, and are thus sharply delimited from the surrounding cytoplasm. The contents of the nucleus are not homogeneous. One or more spherical bodies, the nucleoli, may often be seen inside it. These, although often very prominent, are of subordinate importance, inasmuch as they chiefly represent reserves of material to be drawn on at periods when the nucleus is undergoing division. The more solid gelatinous matrix (*linin*) contains the most important nuclear constituents. A more or less finely divided substance distributed in the gelatinous matrix often gives the nucleus a rather granular appearance. Stains of various kinds render this much more evident, and the stainable particles are often known as *chromatin*.

When the nucleus is about to divide, striking rearrangements are observed to take place within it. The gelatinous linin, in which the chromatin is diffused, contracts, and at the same time the chromatin increases in quantity. Stains of various kinds show that the chromatin-containing strands are, as it were, becoming individualised within the nucleus, although anastomoses between adjacent strands are still of common occurrence. As the strands continue to differentiate, the chromatin is seen to form two parallel streaks in the convoluted linin bands, but this duplex appearance becomes temporarily obscured, though not obliterated, at a somewhat later stage. Each one of these duplex chromatin-containing linin bodies is a *chromosome* (Fig. 26). When fully formed, the chromosomes assume the form of rods, hooks, etc. The most striking point about the chromosomes lies in the fact that their *number is normally quite constant* for a particular species of plant.

The chromosomes become clustered in a very characteristic position, and form a zone or plate across the centre of the nucleus; but preceding this arrangement, and intimately connected with it, a remarkable spindle-shaped structure arises in the extra-nuclear protoplasm (cytoplasm). It is made up of fibres which are ultimately arranged in very much the same curves as iron filings take up when scattered on a piece of paper under which lie the poles of a horseshoe magnet. The spindle-like structure extends across the space originally occupied by the nucleus, while the wall of the latter usually (but not always) disappears, and the only nuclear structure that

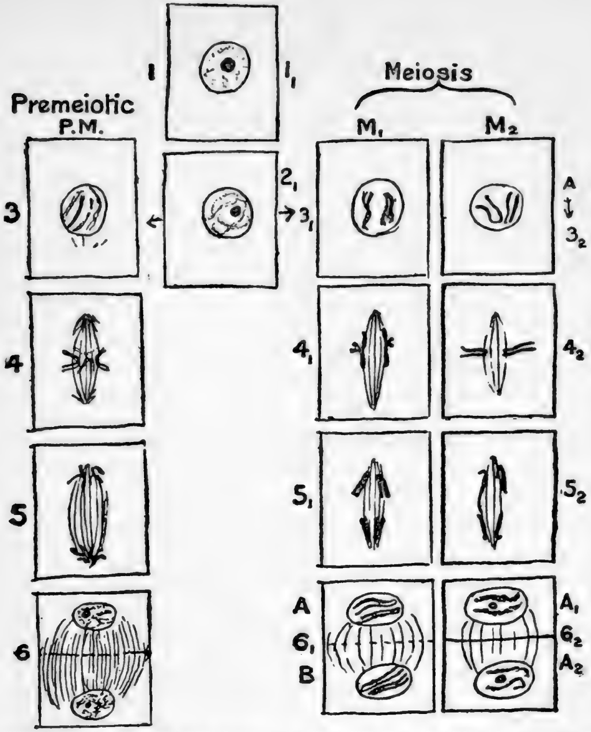

Fig. 26.—Diagram to explain the course of an ordinary nuclear division and the relation to it of the meiotic divisions.

The series 1–6 P M represents selected stages, in the order in which they occur naturally, of an ordinary nuclear division *before* reduction in the number of the chromosomes has occurred.

The series $1_1$–$6_1$ M represents the stages which roughly correspond to the premeiotic in the *first* meiotic (reduction) division. Stages 1 and 2 are practically identical. In 5 the longitudinal fission previously seen in 2, is again clearly visible.

The series $3_2$–$6_2$ ($M_2$) represents the *second* meiotic division. It shows the subsequent division of nucleus A ($M_1$–$6_1$) in the series immediately preceding $M_2$. The corresponding nucleus, B, in series $M_1$ 6, is not shown, but its further division is exactly like that of A.

When A (or B) in $M_1$ 6 proceeds to divide, it does so without going through the stages 1–2, but passes at once into A$3_2$. The sides of each loop represent the early longitudinal fission of the previous series now becoming effective. At $4_2$ the halves are seen in pairs and they separate in $5_2$; in $6_2$ is shown the stage at which the nuclei $A_1A_2$ are finally going back to a resting condition.

persists are the chromosomes. These bodies, as already indicated, take up a very definite position, and now lie in an equatorial plane half way between the two poles to which the spindle fibres converge.

Each chromosome then divides longitudinally into two symmetrical halves, probably along the line of the parallel streaks of chromatin described above. The two halves then diverge, and the *daughter chromosomes* at once retreat along the spindle fibres, to form two groups, one at either pole. The daughter chromosomes swell up, a nuclear wall is formed around them, some of the substances which escape from them run together and form new nucleoli, and thus the two daughter nuclei are formed. A cell wall is often developed across the spindle which persists for a time between the two nuclei which have thus been constituted, and nuclear division is then followed by cell division. When the cell wall is not so formed, a binucleate, or later a multinucleate, arrangement is produced.

The main conclusions that emerge from a consideration of the facts thus briefly outlined are: (1) The number of the chromosomes is constant, and individual peculiarities in form and size are seen to reappear whenever the chromosomes are sufficiently contracted as to become sufficiently clearly recognisable. (2) The chromosomes, when they divide, transmit their peculiarities to each daughter chromosome. In other words, the chromosomes are constant in qualities and properties from one cell generation to another. (3) Owing to the mode of division, and distribution of the chromosomes at a nuclear division, the two daughter nuclei are, to all appearance, exactly alike, each is the reflected image of the other. Subsequent dissimilarities in size, and likewise in other respects, are not excluded, but these are almost certainly of secondary importance.

What does all this mean ? We cannot as yet give a complete answer to the question, but a consideration of the events connected with the differentiation of the sexual cells will perhaps serve to throw some light on the problems involved.

In the first place, we have seen that the sexual act consists essentially in the fusion of two nuclei. How, then, can we reconcile this with the circumstance that the number of chromosomes is constant in the cell nuclei ? For it is evident that the nucleus of each fertilised egg must contain twice as many chromosomes as those present in the nucleus of each of the fusing gametes.

The solution of this problem is furnished by a most remarkable nuclear division which is invariably intercalated somewhere in the series of nuclear divisions that intervene between the first formation of the embryo at fertilisation and the final production of sexual cells which closes the life cycle of the organism (Fig. 26, 1–$6_1$).

In this particular nuclear division we find that the chromosomes are not longitudinally divided and the moieties then distributed between the two daughter nuclei, but that the whole process is carried through in another way.

The earliest stages resemble those of an ordinary vegetative nucleus which is about to divide. The chromatin-containing gelatinous strands make their appearance, and the chromatin is arranged in parallel streaks. But instead of going on to differentiate and finally to divide, the chromosomes proceed to *unite in pairs*. We have very strong grounds for believing that in no case is this union a chance one, but that a chromosome descended from one contributed by the sperm unites with another corresponding to it but derived from the egg. In other words, each pair consists of a chromosome of maternal and a paternal origin.

The net result, then, of the approximation and union of the paternally and maternally derived chromosomes to form the respective pairs is, of course, a reduction to one-half of the number apparently present.

Each pair now behaves as if it were a single chromosome. They flock to the equator of the spindle, but when they divide there, what happens is simply a *disjunction of the two members of each pair*, one of the members retreates to one pole, the other one to the other pole. Hence a *real* reduction is now effected, for each of the two daughter nuclei receives *entire* chromosomes, but of course the original number, now shared between two nuclei, is really reduced in each of them to one-half of what it originally was in previous nuclear divisions.

It will be remembered that prior to the temporary union of the chromosomes to form the pairs, each one of them showed indications of longitudinal fission. It is of special interest, then, to find that immediately on the formation of the daughter nuclei, in the way just described, this fission becomes operative. For a second division supervenes in each daughter nucleus, and so four nuclei are produced. The reduced number of chromosomes in each nucleus is, of course, maintained. Indeed, it invariably happens that *all* nuclei which are derived from one in which reduction has occurred only possess the halved quantity. *It is not until the union of the sexual cells takes place that the original number is again restored.*

The term meiosis has been applied to this process of reduction, and meiosis occurs in every animal and plant which reproduces itself sexually (with possible exceptions, perhaps, in some of the lowest and most aberrant types). Not only so, but even the details of the process are remarkably similar in the many species of animals and plants which have been studied.

Now it is hardly possible that a process so complex, so clearly related to the sexual act, and so similar in its details in the animal and vegetable kingdoms alike, can be devoid of significance. It emphasises the individuality of the chromosomes in the strongest way, and in this respect it is in accordance with results of many experiments which indicate that the chromosomes are, as a matter of fact, different from one another, *i.e.* possess an individuality of their own. Moreover, we see that in the nuclei before meiosis, the chromosomes are present as pairs of homologous individuals, the individuals of each pair having originated, one from the sperm, the other from the egg, at the act of fertilisation to which the plant owed its existence. Furthermore, there is a considerable body of evidence to show that the chromosomes in some way represent the agents by which hereditary qualities are transmitted from each parent. Meiosis provides an obvious method by which the qualities, through the agents that are responsible for them, may be shuffled in the sexual cells; and, as a matter of fact, when hybrids are inbred, or when plants are crossed with one another in a variety of ways, we find the results agree in practice very closely with what is deduced as possible from a study of the behaviour of chromosomes. Indeed, it is not going too far to say that in meiosis and fertilisation we are witnessing the chief act of distributing and recombining the very substances which determine the possibilities of future development on the part of the offspring.

Naturally, the whole story of the nucleus in its relation to heredity is a very long one, and in this brief sketch it has not been possible to attempt more than to indicate, in the barest outline, a few of the most important features of meiosis and of fertilisation.

Meiosis has, however, a further claim on our attention, inasmuch as it has served as the starting-point for some of the most striking morphological developments in the whole series of higher plants.

It has been seen that sexual cells cannot, as a rule, arise until after the nuclei have undergone meiosis. It might, perhaps, be expected that immediately the meiotic phase is over, the four cells which result from it would at once become sexual gametes. In animals this commonly is the case—for in the male animal the four sperms arise by the direct transformation of the cells and nuclei that have just passed through meiosis. In the female the same is true, for the ripe egg, together with the three transitory polar bodies, form the corresponding female gametes. Of these, however, only the egg is normally functional.

In plants, on the other hand, the four cells formed at meiosis never differentiate directly into sexual cells—at least no instance of their doing so is yet known. Often a long series of cell generations intervenes between meiosis and the formation of gametes. The four cells formed at meiosis often separate as four spores, each of which may give rise to a new plant destined in time to produce gametes. Thus meiosis in plants has come to be associated with a special kind of reproductive multiplication which is sometimes called *asexual reproduction.*

It would be better to replace the terms sexual and asexual reproduction by the terms gametic and meiotic reproduction, and thus do away with a misleading antithesis. For " asexual " and " sexual " reproduction are parts of one process, carried through in two stages. The two phases of reproduction, gametic and meiotic, in all the higher plants are associated with two distinct stages in the life history. One of these begins with the fertilisation of the egg, and ends in the meiotic divisions. The spores, which are formed as the result of meiosis, inaugurate the second stage of the life history in which the differentiation of sexual cells takes place.

This rhythmic *alternation* of a spore-producing with a gamete-producing generation is well illustrated by the fern. Starting with the fertilised egg, an embryo is produced, which grows into the ordinary fern. If the backs of the leaves are inspected, brown spots or stripes may often be seen, and these are found to consist of small capsules or *sporangia.* A young sporangium contains a fairly definite mass of internal cells which are enclosed by nutritive tissues, the whole being encased by the sporangial wall. The central cells increase, and whenever their nuclei divide, the full, unreduced number of chromosomes can be seen, just as it may be observed in any other dividing nuclei of the fern plant.

But a time arrives when the central cells within the sporangium become free from each other. Each one proceeds to grow, and it finally divides twice, to give rise to four spores. It is during these two divisions that the reduction in the number of chromosomes takes place in the manner already described, and hence the nucleus of each spore only contains half the number of these nuclear structures. When the spores are ripe the sporangium bursts and the spores are scattered. If they happen to alight on a suitable spot, they germinate, but they do not bring forth a plant like a fern (Fig. 27). A filamentous body is formed which gradually develops into a heart-shaped green expansion known as a prothallus. It is very delicate, and is easily dried up, and consequently is only suited to live where conditions of moisture prevail.

The prothallus sometimes multiplies *vegetatively*, by the dying off of part of the plant, while the living fragments grow into new prothalli. Sexual organs, called antheridia and archegonia, are developed on its under side. In the former a number of sperms are produced, while each archegonium, when mature, contains a single egg. We need not enter into the details of their development, but we may note that each is a specialised cell—not only are the two gametes different from each other, but they are different from all the other cells of the prothallus. Each consists of a naked mass of nucleated protoplasm, but while the sperm consists mainly of nucleus, the egg contains a very large amount of cell protoplasm. We do not as yet know exactly on what the definitely

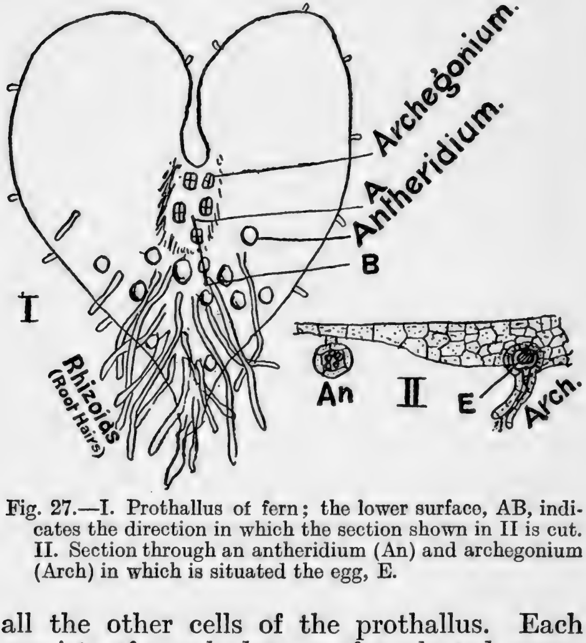

Fig. 27.—I. Prothallus of fern; the lower surface, AB, indicates the direction in which the section shown in II is cut. II. Section through an antheridium (An) and archegonium (Arch) in which is situated the egg, E.

sexual nature of these two kinds of gametes depends, but it seems pretty clear that it is connected with the shedding off of some substance during the course of their development.

When a sperm unites with an egg, the life history enters on the "fern" stage. The fern plant, like the prothallus, may undergo vegetative multiplication in various ways, but sooner or later this "asexual" generation normally culminates in the production of spores, just as the prothallial generation closes with the production of gametes. But the fern does not always go rigidly through these stages in a perfectly invariable manner. We are acquainted with a number of kinds in which the spore-bearing fern leaf may grow out directly into a prothallus. Sometimes a prothallus sprouts from a sporangium, and then all the spores die away. Furthermore, these prothalli may bear male and female sexual organs, and from the egg a new fern plant may arise. What has become of alternation of generations in such a case, and how are meiosis and fertilisation respectively affected ?

Taking the second point first, it may at once be said that prothalli formed in this way resemble the fern in that their nuclei *have not undergone reduction.* Meiosis has been omitted from the life history. But as a consequence of this, the egg is already provided, as also are the sperms, with a double set of chromosomes. It invariably happens, so far as at present is known, that when the eggs are fertile at all they produce new ferns *directly*, that is, *without fertilisation*. Moreover, even the tissue cells of such a prothallus may change their mode of growth, and develop into fern plants without the definite production of sexual organs at all.

Such a departure from the normal course of life history strongly emphasises the relation of meiosis to fertilisation, but it does more than this. It indicates that the striking difference between the fern plant and the prothallus is not itself *essentially* bound up with those nuclear changes which are intimately associated with the sexual phases. It points rather to the conclusion that in these plants the life history, with its two different stages, may have developed in *coincidence*, though not in causal connection with the separation of the sexual process into two stages. It would clearly be futile, in the face of the evidence, to attempt to maintain the existence of a *causal* relation between the nuclear changes and the characteristic differences between the two stages of the life history of the fern. In this way we may understand the continuance of the alternate appearance of fern and prothallus, even when the cellular rhythm no longer obtains.

Considerations of space preclude the following up of this matter in any detail; it may, however, be said quite generally that wherever fertilisation recurs meiosis is never omitted,[1] and this is true for animals as well as for plants. The ordinary course of life histories has been developed long after sexuality and meiosis appeared, and has progressed independently, and on different lines in different groups. Sometimes, as in the higher plants, the stages of the life history are more or less obviously connected with these nuclear cardinal points, at other times the relation is not so evident. For example, it may happen, as in many of the flowering plants, that the two stages in the life history so well separated and analysed in the fern, become curtailed. This happens when the cell which should give rise, by the two divisions, to four spores, cuts the process short, grows, and itself becomes the spore without any division. Such a short cut is taken in certain of the sporangia (ovules) of a lily, orchis, and many other plants. But meiosis is not cut out. It supervenes at the very next divisions which follow the omitted stages during which it would normally have been effected.

As we advance to types of plants above the ferns we find the life history becoming more complicated and less diagrammatically clear. The principle which underlies the complication is, however, a simple one; it consists in a provision for giving the sexually produced embryo an advantageous start in life.

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[1] The occasional anomaly reported for certain mosses requires further investigation.

Even among plants nearly related to the ferns we find that the prothalli produced by the spores tend to differ in their capacity for growth. Those which are destined to produce eggs are large and well stocked with food, those which will produce the sperms are small. This difference becomes reflected in the spores, and even in the sporangia.

In the Selaginella plants, often grown in greenhouses, certain of the sporangia produce a large number of small spores, whilst others become much larger, but only bring a very few (usually four) large spores to maturity.

The small spores form a rudimentary prothallus and a larger or smaller number of sperms. It is essential that the number of small spores should be kept up, so as to maintain a fair chance of a sperm from one of them reaching the relatively few available female prothalli.

Passing to the flowering plants, it is difficult at first sight to realise that we are only witnessing the final stages of an evolutionary development of the structures so clearly distinguishable in the fern. But so it is, and it will be of interest to trace, even briefly, and in spite of the wide gaps, the points of resemblance between them.

The obvious starting-point in both cases is the fertilised egg. The fern plant and the flowering plant each spring from this source. The fern closes its life cycle by producing spores in the way we have seen. The flowering

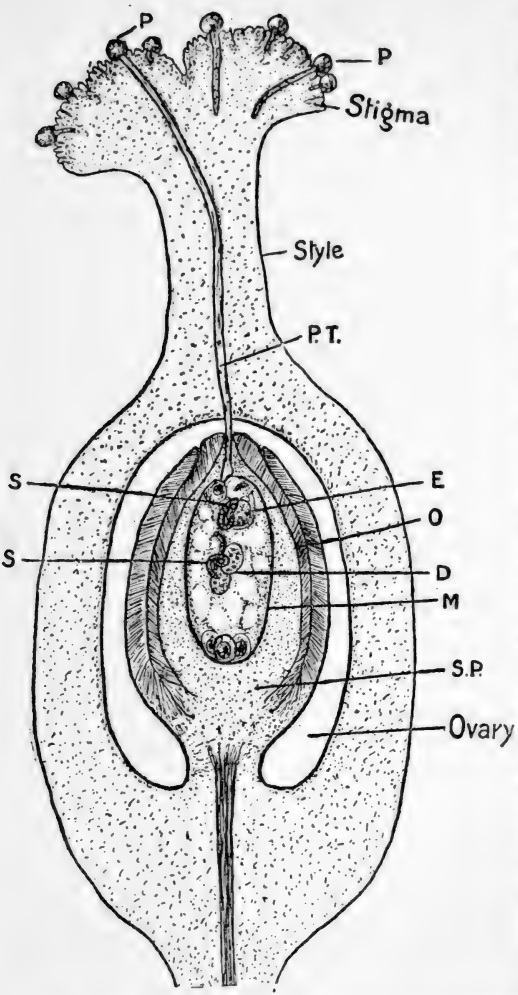

Fig. 28.—Longitudinal section (slightly diagrammatic) through the pistil of buckwheat (Polygonum).

D, endosperm nucleus, formed by the fusion of a pair of nuclei as shown; E, egg; M, spore or embryo sac; O, sporangium or ovule; P, pollen grains with pollen tubes penetrating the tissue of the stigma and style, one of them has reached the spore and has discharged into it the two sperms S and S, these are severally fusing with the nuclei from which the endosperm and embryo will originate. P T, pollen tube.

plant does the same, but the subsidiary events that have happened during its evolution obscure its record. However, we find two kinds of sporangia, one commonly grouped in a cluster of two or four, and forming the so-called pollen sacs borne on each of the stamens. The pollen sacs produce the spores or pollen grains in much the same way as the spores are formed in a fern. But the other sort of sporangium is less easily recognised (Fig. 28). It is often known as an *ovule*, and the ovules are situated inside a closed cavity called the ovary, which forms the lower part of the pistil of the flower. Each ovule (or sporangium) usually contains but one spore, and this is not, like the pollen grain, thrown out of the sporangium, but germinates inside it, and produces an egg as well as a number of other cells. Moreover, the sporangium is retained within the ovary, and hence the methods of fertilisation which are appropriate for a fern would clearly be impossible here. As a matter of fact, the pollen grain, *i. e.* the spore from which the male gamete will be derived, has to be brought into special relation with that part of the flower in which the ovule is situated. At the summit of the ovary there is a specialised structure called the stigma. This is often viscid just when the ovules are mature, and thus any pollen which falls on to the stigma is retained.

The pollen grain or spore already contains developed within it a very rudimentary structure which it is possible to trace back to an extremely reduced prothallus. The pollen grain presently begins to put forth a tube which grows into the tissue of the stigma, feeding, like a fungal hypha, on the juices it contains. The tube grows down through the intervening tissue of the style into the cavity of the ovary. When it reaches this it is attracted to the tips of the ovules, and enters one of them by way of a little pore (the micropyle), burrowing through an intervening tissue of the sporangial (*i. e.* ovular) wall that may be present, until it reaches the spore.

Meanwhile, from the body of the pollen grain the essential structures above alluded to have entered into the tube. Two sperms are developed, but they are not provided with locomotory cilia. They are finally discharged into the cavity of the spore, when they at once lose all cytoplasmic investment, and appear as naked nuclei, somewhat vermiform in appearance. They pass through the protoplasm, which is contained in the spore (or embryo-sac as it is often called), apparently by autonomous movement, and one of them approaches, and finally fuses with, the egg. The other one fuses with a remarkable pair of nuclei which are found near the centre of the egg, and the nucleus resulting from the latter fusion is responsible for the production of the nutritive matter that later on fills so many seeds and grains (*e. g.*

wheat) with "albumen" or endosperm. It is a very remarkable fact, this second fusion. The sperm nucleus which takes part in it is the sister nucleus of that sperm which fuses with the egg. Hence it might be expected that it would carry paternal characters, and that these might make themselves felt in the nature of the endosperm to which the triplicate nucleus gives rise. It turns out that the expectation is realised, and where the endosperms of the pollen parent and the seed parent differ in a well-defined character, *e. g.* in colour or sugar contents, the character imported by the sperm from the pollen may dominate the whole endosperm. Thus, when pollen grains of different varieties of Indian Corn are blown on to a female ear, the endosperm of some of the grains will be found to be affected by the characters borne by the strange pollen. And it is just these identical grains that will betray evidence of hybrid characters in the embryo which each of them contains. For the same pollen grain provided both the sperm for fertilising the egg, and also the second sperm which formed part of the triplicate combination from which the endosperm originates.

When fertilisation has been accomplished, remarkable changes are produced, not only within the ovule, but outside it as well. Within, the endosperm arises, by the repeated division of the triplicate nucleus as already explained, while at the upper end of the ovule the embryo begins to develop. Gradually the ovule changes into the seed. Reserve materials of food accumulate within it, and are most frequently stored either in the growing endosperm, or partly (seldom wholly) in the sporangium wall (nucellus, perisperm). If the embryo reaches any considerable size within the seed, it may presently destroy these tissues, and absorb the nutritive contents into its own body. When this happens, some part of the young plantlet usually becomes thickened and so forms the repository for the food. Most commonly it is the seed leaves (cotyledons), as in the bean, or it may be the young stem below them, as in the brazil-nut, which thus becomes charged with the reserves of food.

In whatever way the food material is disposed, however, it is always so situated as to be readily available when the young plantlet starts into growth, on the germination of the seed.

It does not invariably happen that considerable stores of food after this fashion await the embryo on its awakening to its new life. Many of the flowering plants have followed other lines than that of transmitting to a relatively small posterity large accumulations of hereditary capital. The commonest alternative is seen in the production of vast quantities of small seeds. The seed and the contained embryo have been well cared for during the earlier stages—but they are cast out from the parent plant with the scantiest supplies of ready-made nutriment. Hence, on germination, they must quickly begin to make their own living.

Both methods have proved successful in different lines. The advantage of small seeds lies in the number of offspring produced, and in the ease with which their dispersal is ensured. Of course, it is inevitably accompanied by great mortality—a waste in so far as the individuals are concerned, but by no means necessarily so from the point of view of the race.

Parasites generally (though not invariably) produce huge quantities of small seeds. The profitable result is sufficiently obvious, for the individual chances of success cannot, at best, be very great—a species that relied on few seeds would, in the majority of cases, be placed at a disadvantage, inasmuch as the conditions of successful development can only be seldom realised. Every unsuccessful individual would naturally be exterminated, and thus, with a scanty progeny the race itself might easily die out. Moreover, the advantage of big seeds is less in the case of a parasite than in that of ordinary plants, because if a seed secures a lodgment enabling the embryo to attack a suitable host, nutrition in abundance is ready to hand. But for those that fail to reach a host, no stock of nutrition, however great, would be of any real avail.

It matters little in what direction we cast our attention on the manifold variety exhibited by plants, the adaptedness of species to their environment is always one of the most striking of their many qualities. But, as we have seen, this adaptedness is intrinsically the result of the inner constitution of the plant, which impels it of necessity to develop in this or that particular manner. Only those plants whose constitutions are such as to cause their development to be adapted to a given environment can flourish under the particular conditions imposed by it.

Adaptedness is often achieved in an indirect fashion, but it must be susceptible of realisation in some way or another if the individual is to survive.

Every species, just as every individual of the species, has to face its critical problems. And the problems of the species are really the same, though sometimes disguised under different forms, as those which confront the individual. The race problems are solved by the individuals, often in a wonderful way. Thus many tolerably heavy fruits are dispersed by a wing-like outgrowth which delays their descent to the ground. But at an earlier stage this wing-like outgrowth is generally green, and so may well have helped in the nutritive processes. We can state with confidence that it was not developed *in order to aid* in the dispersal of the fruit, but that it arose as the result of far backward-reaching correlations of ultimate structure and chemical processes within the parent organism. Incidentally, however, as the wing-like structure dries up, its adaptedness for assisting dispersal may become of inestimable value to the species.

The individual has its duty to itself, and its own immediate success is measured by the completeness with which it is adapted to overcome the difficulties that beset it—difficulties that arise partly from within, and partly also from without—and so to emerge victorious in the struggle for existence. But unless it is so constructed as to launch a successful posterity on the world, its race is destined in the long run to perish, and "The place thereof shall know it no more."

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